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The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. It is available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

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Reuben Lasker: A REMEMBRANCE 1929 - 1988

THIS ISSUE OF THE Fishery Bulletin *is in memory of Dr. Reuben Lasker who, until his death, was Chief of the Coastal Fisheries Division of the Southwest Fisheries Center, National Marine Fisheries Service. The contributors and I feel both a debt of gratitude and a strong bond of friendship to this scientist who profoundly influenced our investigations, our careers, and the field of marine larval ecology. Our regret is that Reuben will not see this tribute.*

Andrew E. Dizon, Ph.D.
Scientific Editor

It is the spring of 1989 in La Jolla, California, almost a year since our friend and colleague, Reuben Lasker, left us after a valiant battle against cancer. We remember him fondly, with respect and admiration for the man and for the scientist whose intellectual honesty and humanity endeared him to his associates. We, therefore, dedicate this Festschrift to the memory of a remarkable human being, a warm and caring man, who combined a lifelong passion and dedication to the marine sciences with a bright intelligence, a lively curiosity, and an abiding appreciation of the world around us.

Reuben was born in Brooklyn, New York, December 1, 1929, the only child of Theodore and Mary Lasker. As a child he contracted rheumatic fever, and as was customary at that time his doctors prescribed bed rest for an extended period, when Reuben read avidly. The illness, which left Reuben with a slight heart murmur, influenced his activities and increasingly the boy turned to bookish pursuits. He did well in school, attending the prestigious Boys' High School in Brooklyn, graduating at 16. Because of his health, his father decided that Reuben should go to college in Miami, Florida, to escape the rigors of the severe winters in New York. Accordingly, in 1946, Reuben enrolled at the University of Miami as an English major.

Midway through his college career, Reuben switched his major to zoology with the thought of becoming a medical doctor and in fact actually served as president of the premed society. He received his B.S. degree with honors in zoology, with a minor in chemistry, from the University in 1950. When a graduate research fellowship became available in marine biology, Reuben made a fateful career decision to abandon medicine and applied for the post. He was awarded a full tuition scholarship with stipend for studies in marine biology at the University of Miami where he concentrated on studies on the physiology and cellulose digestion in the shipworm, *Teredo*. He was granted his M.S. in marine biology from the University of Miami in 1952.

Approaching the end of his fellowship at Miami, Reuben began to investigate options for continuing his graduate education. He corresponded with the physiologist, Professor Arthur C. Giese of Stanford University, who had an ongoing marine program at the Hopkins Marine Station. With Giese's encouragement Reuben applied for and was granted a predoctoral fellowship from the National Institute of Health for his doctoral studies at Stanford University. Initially, Reuben was given a small stipend to study the nutrition of the plentiful sea urchins around Monterey Bay. With his young wife, the former Caroline Hayman, the couple drove west in their 1941 black Ford sedan.

Reuben spent the years from 1952 to 1956 on the Stanford campus in Palo Alto researching and writing his doctoral thesis on cellulose digestion in the silverfish. He picked his doctoral topic by chance, although he believed in Pasteur's maxim that chance favors the prepared mind. As Reuben

Opp. page, left: Dr. Gotthilf Hempel of West Germany took this relaxed picture of Reuben during a visit to his laboratory in Building T-21 on the Scripps campus in 1963.

Opp. page, right: Examining a 1 m CalCOFI plankton net in 1965 on the deck of the Bureau of Commercial Fisheries research vessel, *Black Douglas*.

Right: Reuben receiving the U.S. Department of the Interior Silver Medal in 1970 as Gerald V. Howard, Regional Director of the Southwest Region and Alan R. Longhurst, Director of the Fishery-Oceanography Center look on.

was fond of telling the story, he was sitting in a gloomy roomette where the only object left by the former occupant of the cubicle was a box of tissues used in laboratory work. When he reached over and pulled one out, an insect fell down to the table top, skittered away, fell to the floor and disappeared into a crack. The tissue was full of holes and he realized that what he had seen was a silverfish who had made a meal of the paper. Cellulose is difficult to digest by most organisms, and the conventional thought was that animals that eat cellulose, such as the cow or termites, have microorganisms in their stomachs to do the digesting for them. Reuben reflected that since no one had ever mentioned how a silverfish did its cellulose digesting, this might be a suitable topic for a Ph.D. thesis. On completion, the thesis was ranked "Superior" by Stanford University and established Reuben's reputation as an authority on the physiology of this insect. He received his Ph.D. degree in biology in 1956.

In February 1956, Science magazine carried a small announcement in its back pages that a meeting, sponsored by the Rockefeller Foundation, was to be held at the Scripps Institution of Oceanography in La Jolla, California on the future of marine biology. A small amount of money had been set aside for graduate students who were asked to apply to Dr. Adriano Buzzati, the convenor. Reuben promptly wrote to Buzzati, explaining that he was a graduate student at Stanford in marine biology and eminently qualified by inclination and interest to attend. By return mail he received a round-trip ticket from Palo Alto to San Diego and a check for $50 "to cover expenses." At the train station in San Diego, Reuben was picked up by Leo Berner, then a graduate student at Scripps and presently a professor and former dean of oceanography at Texas A&M University, who later became a close friend.

Famous names in marine biology were in attendance at the meeting—Albert Szent-Gyorgyi, Nobel Laureate for the discovery of vitamin C; the English biochemist Ernest Baldwin; Eugene Odum, ecologist from the University of Georgia; Roger Revelle, then the Director of the Scripps Institution of Oceanography and later one of the founders of the University of California, San Diego; John Isaacs, professor of oceanography who was destined to have a profound influence on Reuben; and many others who collectively represented the forefront of research in marine biology, worldwide.

Buzzati, a geneticist, was then a professor at Scripps. He offered to submit a proposal for Reuben to the Rockefeller Foundation to culture euphausiid shrimps, a project on which Reuben had been working. On his return to Stanford, Reuben wrote the proposal and by return mail received notice that he had been awarded a post-doctoral appointment for $5,000 a year (tax-free). By the following September, Reuben and Caroline arrived in La Jolla in a car packed with all their possessions.

The project Reuben chose for himself was to attempt to maintain euphausiids in reasonable health in the laboratory and to find out how effi-

Reuben with Walterio Garcia, Jacobo Melcer, and Paul E. Smith aboard the research vessel *A. Humboldt* in 1975.

Opp. page, left: In foul weather gear aboard the University of Alaska's research vessel, *Alpha Helix*, during a research cruise to the Pribilofs in 1982 to study groundfish.

Opp. page, right: Showing off the Huntsman Medal for Excellence in Biological Oceanography awarded him in 1983 by the Canadian government's Bedford Institute of Oceanography.

ciently they used their food. Since no one offered to provide him with live animals to work on, Reuben arranged to go to sea on the Scripps T-boat (the U.S. Army's designation for Transportation), an 80-foot vessel with a 3-man crew. Dosed massively with Dramamine, the former Brooklynite who never learned to swim, was taught how to catch euphausiids by Scripps researchers Elizabeth and Brian Boden. During one particularly eventful trip, Reuben was 10 miles off San Diego where the vessel had been stopped to deploy a plankton net. Alone on deck, in heavy seas and without a life jacket, Reuben remembered the ship giving a sudden lurch that propelled him forward over the chain railing. Fortunately for Reuben he managed to save himself by grabbing a projecting object as the ship steamed ahead at 10 knots away from where he would have been hurled into the sea.

Until he finally figured out the correct dosage of Dramamine, Reuben was very susceptible to sea sickness. Although it was necessary to go to sea to collect live specimens, Reuben preferred to keep his sea trips as brief as possible. Serendipitously, he located an area of the ocean in the lee of Pt. Loma which not only produced euphausiids and fish larvae in abundance but also had the virtue of being relatively calm. This became his favorite spot for collecting specimens and in years to come became well known to his colleagues as Lasker's Lake.

The postdoctoral year went quickly with Reuben who was working on the energy balance of euphausiids and looking for a job. A notable event for the Laskers during this time was the birth of their daughter, Pamela.

It was also during Reuben's sojourn at Scripps that a meeting took place which had important implications for his future. Through a mutual friend he met John C. Marr, Director of the U.S. Department of the Interior's Bureau of Commercial Fisheries, South Pacific Fisheries Investigation, who had recently relocated his laboratory in the old Director's residence on the Scripps campus. Marr was interested in Reuben's work on euphausiids, and some months later when the laboratory was reorganized he asked Reuben to head up a physiology section. Meanwhile, Reuben had accepted a job at Compton Junior College; although it provided him with his first taste of teaching, he informed the dean that he would not be renewing his contract because he wanted to return to research. At the end of the academic year, the Lasker family left Compton and returned to La Jolla, where Reuben had been granted a Lalor Faculty Fellowship at the Scripps Institution of Oceanography. In the interim Marr was able to complete the arrangements for Reuben's recruitment. Accordingly, in June 1958, Reuben entered on duty at the federal fisheries laboratory in La Jolla, as a fishery research biologist. Thus began a creative, productive partnership, an association that lasted through numerous federal reorganizations and changes in research emphases, and which endured until Reuben's death some 30 years later.

In establishing a Physiology Program and

selecting Reuben as its principal investigator, Marr embarked on a major change in the direction of research on pelagic marine fishes. He believed that there were many problems that could be solved only through controlled laboratory experiments. Heretofore, few studies had been made on the physiology of pelagic fishes. It had not been possible, for example, to study the fecundity of sardines and other pelagic fishes under laboratory conditions, since fish held in aquaria were not known to spawn. However, under proper conditions of diet or by control of endocrine development, it was at least theoretically possible to induce normal spawning in aquaria. Marr proposed that Reuben undertake such studies as the investigation of the efficiency of food utilization by larval fish, the influence of various factors on the rate of growth, the change in body conditon during ovarian development, and the like.

With this as a mandate, Reuben moved into T-21, one of the gray clapboard cottages (former residences of Scripps' professors) that dotted the hills around Scripps Institution of Oceanography. With the help of his newly hired assistant, Gail Theilacker, a former graduate student at Scripps, he proceeded to establish a laboratory oriented toward basic research, whose main purpose was the study of the innate and adaptive responses of marine organisms. Although Reuben's main academic interest was the investigation of energy exchanges between marine animals and their food supply, he was also interested in other physiological functions that could affect an organism's ability to survive in the sea.

The Physiology Laboratory in T-21 whirred with activity as Reuben threw himself into his new job, infecting others with his customary energy and enthusiasm. Soon, old white bathtubs with clawed feet were filled with seawater and located inside and outside T-21 to hold experimental animals. A particularly robust colony of brine shrimp and algae flourished as a self-contained ecosystem in yet another outside bathtub. One of the first high-speed Beckman ultracentrifuges, used to separate different sardine proteins, hummed upstairs. In another room a continuous oxygen measurement system, using one of the first double electrode probes, which had been invented by Reuben's close friend and colleague, Dr. John Kanwisher, of the Woods Hole Oceanographic Institution, produced quantities of exciting data.

Because government funds were scarce, Reuben took every opportunity to take advantage of federal government surplus property to equip his laboratory for experiments on respiration and energy uptake of sardine eggs and larvae. In the absence of a proper cold room, he located a meat packer's cold locker and set this up outside the building. Another piece of equipment picked up from government surplus lists was a hot dog cooker that had small, rotating aluminum rods to heat the wieners. This, minus the heating element, was adapted by Reuben and Gail to turn syringes

filled with sardine eggs rather than wieners. In his enthusiasm to properly study respiration in sardine eggs directly from the sea, Reuben and Gail even installed their Warburg respirometer, without the cooling and shaking system, on the Bureau's old research vessel, the *Black Douglas*, reasoning that the continual shaking motion of the ship would adequately mix the eggs with seawater. Since the work required a constant cold temperature, the only location that met the requirement aboard the *Black Douglas* was deep within the bowels of the ship, accessible only by crawling into the confined space on hands and knees.

It was also about this time that the Cahn electrobalance, now a staple of well-equipped laboratories was developed. The inventor himself set up the equipment in Reuben's T-21 where it was used for weighing individual sardine eggs and larvae. Reuben also took pride that he was one of the first scientists to use the carbon-hydrogen-nitrogen analyzer, and in fact field tested it for the company manufacturing the equipment.

The laboratory soon became a magnet for visiting scientists, investigators, and graduate students. During the summer months, high school students labored at various tasks, measuring euphausiid lengths, collecting limpets, and extracting substances from the tube feet of starfish. From his vantage point at a large wooden desk before a picture window with the panorama of the California coastline curling north, Reuben supervised this activity, while continuing to author or co-author numerous papers on energetics of euphausiids, energetics of sardines, physiology and ecology of fish larvae, and ultimately to studies of the mechanisms underlying recruitment of fishes.

In 1963, Reuben organized a symposium on larval fish biology that would encompass topics ranging from systematics of fish larvae to the technology of fish rearing to the basic physiology of single fish eggs and larvae. In the process Reuben forged close personal and professional links with many of the scientists who attended—James Shelbourne of the Fisheries Laboratory in Lowestoft, England; Gotthilf Hempel of the Institut für Hydrobiologie of the University of Hamburg; J. H. S. Blaxter and F. G. T. Holliday of Aberdeen University; and others—associations which continued throughout his life.

In 1966, Reuben and his family, which now also included a son, Paul, traveled to Aberdeen, Scotland to work at the University of Aberdeen for one year with Blaxter and Holliday. Here Reuben applied the techniques perfected in his work on euphausiid shrimps to the study of the food chain in an experimentally developed fishery, utilizing hatchery-reared larval and juvenile plaice. The year in Scotland with his family proved to be one of the happiest in Reuben's life, leaving him with an abiding affection for all things Scottish.

In October 1964, the Bureau of Commercial Fisheries, Fishery-Oceanography Center, as it was then called, was completed, adjacent to the campus of the Scripps Institution of Oceanography. It was an imposing structure of four concrete buildings grouped around a central courtyard, 220 feet above the Pacific Ocean. The gray cottage, T-21, site of many research accomplishments, was abandoned. Reuben and his staff moved into a wing of the Center which was equipped with the most modern equipment and perhaps most importantly gave access to an experimental seawater aquarium with temperature control rooms for physiological studies and rearing experiments, all of which Reuben helped to design.

With the move into his well-equipped new laboratory, Reuben assembled a dedicated cadre of behaviorists, physiologists, oceanographers, population dynamicists, and experimental biologists. At this point in his professional life he had already established a solid basis of scientific achievement on which others could build. His work on the energy exchange between fishes and their food supply, his work on osmoregulation by sardine embryos and larvae, and his work on the effect of temperature on the growth and development of both sardine and anchovy larvae were fundamental to understand the dynamics of fish populations and provided the scientific rationale for the project to rear pelagic marine fish in the laboratory. Subsequently, under Reuben's direction and leadership, more than 30 species of pelagic fishes, including the commercially valuable sardine, anchovy, and mackerels, were reared from eggs, through larvae, to subadult stages, for the first time ever in a laboratory. Reuben's papers on marine invertebrates and on the energy budget of clupeids in relation to their planktonic food were widely read and quoted. His

paper on the feeding, growth, respiration, and carbon utilization of a euphausiid crustacean became a citation classic (Current Contents, 1983, Volume 14, page 17).

With outstanding researchers and equipment, particularly the facilities of the experimental seawater aquarium, at his disposal, Reuben was able to concentrate his research on ecological and physiological factors that would help answer one of the most important and fundamental questions in fisheries: What determines how many young fish will survive the rigors of life in the sea to become reproducing adults?

Ever the creative and imaginative scientist, Reuben constantly came up with fresh and innovative scientific approaches. An example was an experiment in which he took anchovy larvae spawned in the Center's seawater aquarium to sea in order to test his idea that laboratory-raised anchovy could be used in lieu of naturally spawned larvae as an assay of conditions in the sea.

Another remarkable idea came to Reuben when he was on a cruise to sample patches of larval food. Following a storm with strong winds that mixed and diluted the dense layer of larval forage from which he had drawn his samples, it occurred to him that upwelling events and storms are detrimental to fish larvae because these events dilute concentrations of larval food. He suggested that larval survival increases during periods of weak winds when the coastal seas stratify and the forage of larval fishes concentrates in layers. This "stability" hypothesis has greatly interested oceanographers and fishery biologists both in this country and abroad and has stimulated efforts of individual researchers to study the definitive links between fish larvae and their microenvironment. Now known as "Lasker Events" (see following article on "An eponym for Reuben Lasker" by Daniel Pauly), these calm periods could be the key factor in larval survival, and ultimately recruitment.

The years passed quickly and happily for Reuben. As Chief Scientist of what would become the Coastal Fisheries Resources Division, he directed the efforts of a multidisciplinary research team and was signally successful in stimulating and inspiring his staff to pursue promising avenues of research. This record of research achievement received mention in the review conducted by the National Academy of Sciences in its evaluation of the National Oceanic and Atmospheric Administration's ocean research and development. The examiners wrote, "The Coastal Division represents a center of excellence . . . the Division has a high scientific awareness, much talent and enthusiasm, and is doing some excellent research."

One remarkable example of how Reuben's leadership and influence led to a major breakthrough is his role in developing the estimation procedure for anchovy biomass assessment. He was among the first to recognize the unique potential of this method and was responsible for bringing together the disparate disciplines and people that made it work. The method permits the estimate of biomass from the ratio of the egg production rate in the sea to the daily fecundity of the spawning fish stock. This new method of pelagic population analyses was accomplished by a team effort and was founded almost entirely on previous research done by Reuben and others, research which provided the essential background information on which to build. In order to develop the anchovy biomass assessment, a wide variety of studies on sampling, statistical methodology, fish biology, ecology, behavior, and physiology had to be made. All of these studies added greatly to the knowledge of clupeoid biology.

As of this writing, the biomass assessment method has been incorporated into the Northern Anchovy Management Plan as a guide for setting anchovy fishing quotas in the coastal waters of the U.S. Pacific Coast and has been adapted in other countries such as South Africa and Peru. It is increasingly viewed by many fisheries scientists as the best current assessment technique for fishes with pelagic eggs.

In 1970, in response to a request from the administrators of the fisheries service, Reuben (with the able assistance of the late Lon Manar as the managing editor) undertook the task, as scientific editor, of revitalizing the venerable U.S. *Fishery Bulletin*. Before 1971, the Fishery Bulletin appeared irregularly for lack of sufficient contributions of merit. Authors sought other journals because it took 2–3 years to get papers published in the Fishery Bulletin. During Reuben's first year as editor, the Fishery Bulletin became a quarterly and the number of pages printed per year almost tripled. Be-

cause of his scientific reputation, Reuben was able to attract to the pages of the Fishery Bulletin not only outstanding contributions from members of the NMFS staff but also major contributions from scientists outside NMFS. He initiated and enforced a peer review system for reviewing manuscripts, not only for the Fishery Bulletin but also for other NMFS publications. His impact on the scientific image, character, and tone projected by NMFS publications was a reflection of his own standards of scientific excellence and personal integrity. The revitalized Fishery Bulletin, an indispensable research journal to those in the field of fisheries, now reaches several thousands of readers worldwide. Reuben's contributions as Scientific Editor were even more remarkable becaues he worked at this job only half-time while continuing his research on fish physiology.

Reuben also served as an essential link to the surrounding academic community, particularly the nearby Scripps Institution of Oceanography with which the fisheries laboratory had long maintained close ties. In 1966 he received an appointment as an Associate Professor of Marine Biology in Residence at Scripps and in 1973 was appointed Adjunct Professor of Marine Biology. He supported and encouraged his graduate students, and participated with his usual enthusiasm in faculty committee work. It was most typical of Reuben that although his strength was sapped by his illness he introduced his last graduate student at a thesis defense several days before his death with humor and wit.

During his 30 years as a government scientist he put together many workshops and meetings which attracted scientists from all over the world and fostered creative collaborative efforts. For example, in recent years, he organized workshops for the Sardine-Anchovy Recruitment Program (SARP) which brought together scientists from all major upwelling regions of the world to develop a practical plan for studying recruitment. Major credit for the active and productive SARP programs that exist today in many parts of the world belongs to Reuben's efforts and interest.

He was a gregarious man who loved people and conversation. He delighted in travel to the far places of the world. Many of the letters received after his death testify eloquently to the warm affection and regard in which he was held by hundreds of his colleagues throughout the world.

During his lifetime Reuben was the recipient of high honors. The U.S. Government awarded him the Meritorious Service Award of the U.S. Department of the Interior (Silver Medal Award) in 1970 and the Distinguished Service Award of the U.S. Department of Commerce (Gold Medal Award) in 1974. The Canadian Government's Bedford Institute of Oceanography awarded him the Huntsman Medal for Excellence in Biological Oceanography in 1983.

Reuben's preeminent role as outstanding researcher, his practical wisdom, wide experience, and knowledge made him much sought after as a prime mover, advisor, and member of many prestigious committees, commissions, and boards where he served with distinction, most recently as a member of the Ocean Studies Board of the National Academy of Sciences.

He maintained close ties with friends and colleagues around the world, through voluminous correspondence and telephone calls. He was ever the optimist and many of his correspondents never realized the gravity of his illness which re-occurred in March of 1987. As his lifelong close friend, Dr. Howard Feder of the University of Alaska wrote later, "I can hear Reuben's voice in my head saying, 'Goodbye, old buddy. Don't be sad. I did everything I wanted; I have no regrets. Remember, Howie, life goes on! Enjoy yourself.'" On April 27, 1988 his friends scattered his ashes from the National Marine Fisheries Service research vessel, *David Starr Jordan*, appropriately enough, in the sea off Point Loma, known as Lasker's Lake.

For those of us lucky enough to have shared this life with him, the thought of Reuben will always bring the warmest memories. As his friend Lucian Sprague wrote, "As long as there are friends who remember him, students to read his papers and to carry on his work, he will be very much with us in spirit."

In the year which followed Reuben's death, his friends organized the Reuben Lasker Memorial Fund. The Fund is administered by the Coordinator of the California Cooperative Oceanic Fisheries Committee (CalCOFI) and is used for travel fellowships for students to attend the annual CalCOFI meeting. Anyone interested in contributing to the

fund may do so by writing to the CalCOFI Coordinator, P.O. Box 271, La Jolla, CA 92038. Also in 1988, the American Institute of Fishery Research Biologists posthumously awarded Reuben their Outstanding Achievement Award for his distinguished lifetime career accomplishments in fisheries science and for his outstanding contributions to research and management.

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An Eponym for Reuben Lasker

Reuben Lasker published in 1975 and 1978 two papers in which he suggested that the maintenance—through a "period of calm"—of thin layers of food-rich patches was crucial to the survival of newly hatched northern anchovy larvae. These papers had an enormous influence on fisheries research throughout the 1980s, as can be easily assessed, e.g., through citation analysis.

Recently, Peterman and Bradford (1987, their note No. 16) operationally defined the periods of calm alluded to above as periods of four consecutive days with wind speed below 10 m s^{-1}. They also proposed to view periods of five consecutive calm days as two partly overlapping 4-day periods, period of six days as three partly overlapping periods, etc.

I recently proposed (Pauly 1987), in a book largely devoted to following up on R. Lasker's work, the term "Lasker events" as an eponym for a period of four calm days with winds less than 5 m s^{-1}. The present volume provides an appropriate context to reiterate and refine this suggestion.

Thus, to allow different authors to identify different hypotheses related to the effects of periods of calm, I propose to use the notation "*i/j* Lasker event" for period of calm lasting *i* days and defined by winds not exceeding *j* m s^{-1}. Thus, e.g., Peterman and Bradford (1987) worked with "4/10 Lasker events", while Mendelssohn and Mendo (1987) worked with "4/5 Lasker events".

This suggestion offers a parallel for the more general "Lasker-hypothesis" now widely used as an eponym for the mechanism proposed by Lasker (1978, 1985).

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Optimal Wind Conditions for the Survival of Larval Northern Anchovy, *Engraulis mordax*: A Modeling Investigation

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ABSTRACT: How the frequency of storm events can influence the survival of larval northern anchovy, *Engraulis mordax*, was investigated by computer modeling. The hypothesis was as follows. While wind events dissipate layers of planktonic food, a total absence of wind mixing would reduce upward nutrient flux and retard plankton production. Therefore, there must be optimal conditions of wind speed, duration, and frequency of wind events for maximum survival of northern anchovy larvae. From numerical experimentation, all wind events were detrimental to post-yolk-sac larvae present in the water column at the time of the storm. However, if initial prey concentrations are insufficient for optimal growth of larvae, then a wind event which increases primary and secondary production may be beneficial to larvae emerging from the yolk-sac stage after the storm. The conclusion was that optimal conditions for larvae survival occur when a wind event strong enough to deepen the mixed layer into the nutricline is followed by a period of calm. This period between storms must be long enough for larvae to develop into a stage where short-term starvation can be endured.

In 1975, Lasker hypothesized that larval anchovy survival was dependent on the stability of the water column. Laboratory work (see Blaxter and Hunter 1982; and references therein) showed that first-feeding anchovy require very high concentrations of plankton food. These high concentrations are found in the upper water column, but only during periods of low winds and reduced turbulence (Lasker 1975; Owen 1989). Recently Peterman and Bradford (1987) performed a statistical analysis of wind and larva mortality data from the field that confirms Lasker's hypothesis. There is a statistically significant relation between larva mortality rate and the frequency of calm, low wind speed periods which permit the maintenance of concentrated patches of food.

However, completely calm wind conditions cannot be ideal, because a stratified water column reduces the vertical flux of nutrients into the euphotic zone, reducing production of plankton (Lewis et al. 1986). Eppley and Renger (1988) recently measured the slight increase in nitrate in the surface layer owing to a moderate wind event in California coastal waters, and found the data consistent with the wind driven, nutrient flux dynamics of Klein and Coste (1984).

Consider the fact that northern anchovy, *Engraulis mordax*, populations off central and southern California spawn mostly during the winter and spring months (Smith 1972; Smith and Richardson 1977), not during the summer when winds are most calm and the water column most stratified by solar heating (Husby and Nelson 1982). The timing of the spawning of these populations may be an adaptation to maximize the survival of larvae.

This is the third in a series of modeling efforts (Wroblewski 1984; Wroblewski and Richman 1987) to simulate the environmental conditions which influence the survival of northern anchovy. Each successive model builds on the previous model by increasing complexity (and realism) in the biological and physical dynamics. Here we investigate by numerical experimentation the manner in which the frequency of storms during the spawning season of northern anchovy could influence survival of larvae. We find there is indeed a theoretical optimum condition of wind speed, duration of event, and frequency of events for maximum survival.

METHODS

Our model investigates the mortality of north-

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ern anchovy larvae for 15 days from first feeding. From histological indications of tissue condition, O'Connell (1980) showed that anchovy larvae less than 10 mm SL are vulnerable to starvation. For northern anchovy, yolk-sac absorption and first feeding occurs 3 to 4 days (depending on temperature) after egg hatching. Larvae obtain a standard length of 10 mm about 19 days after hatching (Blaxter and Hunter 1982). Thus the larvae are subject to starvation for 15 days after first feeding. The larvae metamorphose at 34 to 40 mm SL, about 56 to 60 days after hatching.

O'Connell (1980) suggested that larvae above 10 mm SL may be less vulnerable to starvation because of increasing nutriment (protein, carbohydrate, and lipid) reserves with growth. Early post-yolk-sac larvae have negligible reserves and will survive only two or three days without any food (Lasker et al. 1970; O'Connell and Raymond 1970). Larger (35 mm SL) larvae can survive two weeks of starvation as their lipid content declines (Hunter 1977).

Because of their small mouth size, first-feeding northern anchovy larvae are restricted to feeding on small prey (Hunter 1977). First-feeding northern anchovy are initially able to subsist on a diet of the unarmored dinoflagellate *Gymnodinium splendens* (Lasker et al. 1970). However, after a few days, their growth rate will be greatly depressed unless their diet includes more typical foods of young clupeoid larvae such as tintinnids, ciliates, copepod eggs, naupliar, and copepodite stages (Arthur 1976; Blaxter and Hunter 1982; Theilacker 1987). Therefore, in our model, we consider the prey of young anchovy larvae to be microzooplankton. We do discuss later the availability of *G. splendens* to first-feeding larvae under the turbulent mixing conditions predicted by the model.

Larval Fish Dynamics

Our formulation of growth and mortality of larval northern anchovy (see Wroblewski 1984) is based on the laboratory experiments of O'Connell and Raymond (1970), who determined the effect of various zooplankton prey concentrations on the survival of larvae over the first 12 days of life. The prey in the O'Connell and Raymond (1970) experiments were wild crustacean nauplii with some tintinnids and phytoplankton also present.

The equation for growth rate of larval anchovy expresses the difference between metabolic gains and losses,

$$\text{growth} = \text{ingestion} - \text{egestion and excretion}.$$

Ingestion of prey by larval anchovy is calculated, using the Ivlev (1955) formulation for the feeding of fishes. Egestion of fecal matter by anchovy larvae is taken to be a constant fraction of the ingested ration. Metabolic excretion is assumed to occur at a basal rate plus an additional excretion associated with feeding activity.

Larval anchovy mortality is expressed in the model as a function of weight at age, or in other words, the feeding history of the larvae,

$$\text{mortality} = \text{baseline growth rate/actual growth rate}.$$

Mathematical formulations for larval anchovy growth and mortality used here are the same as equations (5) and (6) in Wroblewski and Richman (1987).

Prey Dynamics

The equation for the concentration and vertical distribution of the prey of larval anchovy (microzooplankton) is one of a set of coupled partial differential equations describing the plankton ecosystem. These equations for phytoplankton, zooplankton, and dissolved nutrient (nitrate) in a one-dimensional water column are given as equations (1) to (4) in Wroblewski and Richman (1987). Analytical solutions to these plankton equations have been derived and sensitivity analyses have been performed so that one can fully understand how the concentration of prey responds to changes in the biological parameter values (see Franks et al. 1986; Wroblewski and Richman 1987).

The biological parameter values used here are the same as in table I of Wroblewski and Richman (1987), with the exception that the growth rate of the phytoplankton is reduced. In the previous study, it was assumed that the average growth rate in the euphotic zone (waters with greater than 1% surface light intensity) was 2 doublings day^{-1}, if nutrients were not limiting. Here we assume that the maximal growth rate of the phytoplankton at the surface is 2 d^{-1}. Below the surface, the growth rate of the plants is given by $V = V_m \exp(-k\,z)$, where V_m is 2 d^{-1} and the light extinction coefficient k is 0.1 m^{-1}. The effect of this change in plant growth rate is to reduce the concentration

of phytoplankton in the water column, so that the simulated profile of phytoplankton (Fig. 1a) more closely resembles the observations off Southern California reported in Cullen et al. (1983) and Mullin et al. (1985).

The modeling studies by Wroblewski (1984) and Wroblewski and Richman (1987) examined how the concentration of prey responds to perturbations in the physical oceanographic environment caused by wind forcing. Wroblewski (1984) used scale analysis to deduce the thickness of the layer of prey which could be maintained during wind-induced turbulent mixing. He found that the effectiveness of turbulence in dispersing food for northern anchovy larvae is lowered by any ability of the prey to aggregate into patches. The conclusion was that first-feeding larvae could find sufficient concentrations of motile *G. splendens* in the pycnocline during moderate wind conditions.

Wroblewski and Richman (1987) coupled the plankton equations to a simplified model of mixed layer dynamics (Niiler 1975) to calculate wind-driven deepening of the mixed layer and the turbulent diffusivity within the mixed layer during and after a wind event. Wroblewski and Richman found that wind events are always detrimental to larval northern anchovy, because wind mixing dissipates vertical structure in prey concentration as Lasker (1975) proposed. However, they discovered that interacting biological and physical processes determine the time interval before high concentrations of prey are reestablished, i.e., the starvation period endured by the anchovy larvae. Reproduction by prey and their aggregation by swimming govern the rate of reestablishment of vertical structure in prey distributions, once wind conditions allow turbulence in the upper water column to dissipate. They noted as significant that first-feeding larval anchovy forage directly on *G. splendens* and microzooplankton which have the reproductive capacity and migration ability to reestablish high concentrations shortly after a storm.

Wroblewski and Richman (1987) were able to quantify the influence of wind event magnitude and duration on larval northern anchovy survival. However, as Niiler's (1975) mixed layer model does not permit restratification of the upper water column by solar heating between wind events, more complex physics was required to explore the influence of interstorm duration on larval anchovy survival.

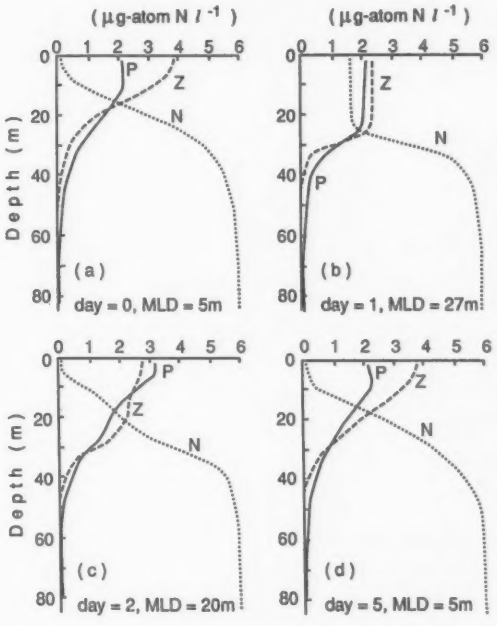

FIGURE 1.—Temporal evolution of the one-dimensional (vertical) plankton model in response to a single wind-mixing event. Initial conditions are the steady state profiles of phytoplankton (P), zooplankton (Z), and nitrate (N) shown in panel (a). The wind speed during the event is 16 m s^{-1} with 24 h duration. MLD refers to the mixed layer depth.

Mixed Layer Dynamics

Here we use the mixed layer dynamics of Mellor and Yamada (1974; 1982) which predict both wind-driven deepening of the mixed layer and shallowing of the mixed layer by solar heating. Heat is absorbed at the sea surface and shortwave radiation penetrates the surface, attenuating exponentially in the manner formulated by Simpson and Dickey (1981).

Klein and Coste (1984) used the turbulence closure scheme of Mellor and Yamada (1974) to study the influence of wind forcing on nutrient transport into the mixed layer, but treated nitrate as a conservative quantity. Chen et al. (1988) used Mellor and Yamada (1974) dynamics with both wind and tidal forcing to simulate vertical nutrient mixing in Long Island Sound, but also considered biological consumption and production of nitrate. We refer the reader to Klein and Coste (1984) and Chen et al. (1988) for details on the implementation of Mellor and Yamada's (1974) level 2.5 dynamics in this type of physical-biological modeling study.

Initial Conditions

The initial conditions for a simulation are the steady state solutions of the plankton dynamics for a stratified water column (Fig. 1a). The initial temperature gradient is 4°C over the upper 100 m. The daily average surface heating is 50 W m^{-2} which is divided equally between short- and long-wave radiation. A background eddy diffusivity of 10^{-4} m^2 s^{-1} throughout the water column is assumed.

RESULTS

Multiple Wind Events

Figure 2 shows the wind speed, level of turbulent mixing at 3 m below the surface, and the mixed layer depth for the simulation where three wind events occur within a 15 d period. Fifteen days is the critical period after yolk-sac absorption when northern anchovy larvae are susceptible to starvation (O'Connell 1980). Each wind event has a wind speed of 16 m s^{-1} and a duration of 24 hours. Between the events, the water column restratifies due to a solar heating of 25 W m^{-2} at the surface and to a short-wave radiation flux of an additional 25 W m^{-2} penetrating the upper 10 m of the water column.

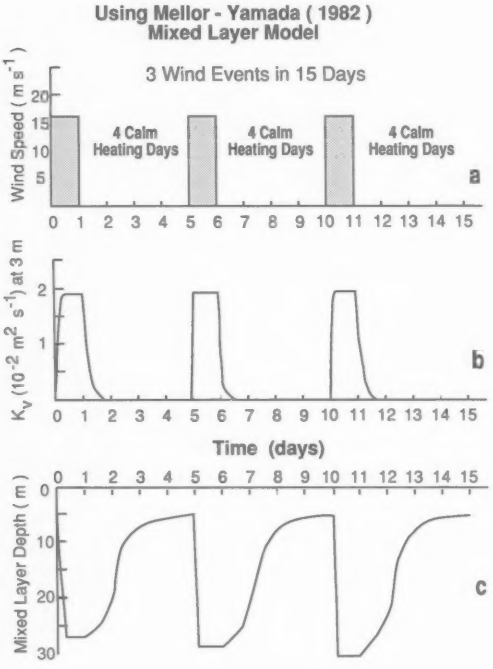
Using Mellor - Yamada (1982)
Mixed Layer Model
3 Wind Events in 15 Days
Wind Speed (m s-1)
4 Calm Heating Days
4 Calm Heating Days
4 Calm Heating Days
a
Kv (10-2 m2 s-1) at 3 m
b
Time (days)
Mixed Layer Depth (m)
c

FIGURE 2.—The wind speed (a), vertical eddy diffusivity K_v at 3 m depth (b), and mixed layer depth (c) during a simulated 15 d period. The Mellor-Yamada (1982) model was used to calculate K_v and the mixed layer depth.

In the Mellor-Yamada (1982) model, the turbulent diffusion coefficient K_v is predicted as a function of depth; it has a maximum within the mixed layer and decreases markedly below. Since we are primarily concerned with dissipation of plankton near the surface where the concentration of prey is greatest (due to high productivity of the phytoplankton), we plot in Figure 2b the value of K_v at 3 m depth over the 15 d period. The deepening of the mixed layer during each event and its shallowing after each wind event is shown in Figure 2c. Note that the mixed layer deepens slightly more with each subsequent event, as the water column does not completely restratify during the 4 d period between each wind event. The background diffusivity maintains a mixed layer 5 m deep.

The model prediction of the increase in larval anchovy mortality for the three wind event case is shown as curve b in Figure 3. For comparison the mortality rate for larvae which experienced only a single event of the same wind speed and duration is shown as curve a in Figure 3. Curves a and b are the same until day 5 when the second wind event begins. The mortality rate for larvae experiencing a second and then third wind event continues to increase with time, while the mortality rate for larvae enduring only one event declines as turbulence in the water column dissipates and food concentrations are reestablished (see Figure 1, panels c and d).

The mortality rate after 15 days for larvae having endured a single wind event is about 6% d^{-1}. If no wind event had occurred, their mortality rate would be about 4% d^{-1} (curve e in Figure 3). Thus a single event does not have a great cumulative effect. However, for larvae having endured 3 wind events over their 15 d development period, the mortality rate increases to 13% d^{-1} (curve b in Figure 3).

The mortality rate increases dramatically with the frequency of wind events. Curve c in Figure 3 shows the influence of 5 wind events each of wind speed 16 m s^{-1} and 24 hours duration on a cohort of larvae reaching the first feeding stage at time zero. The mortality rate at the end of 15 days is 21% d^{-1}.

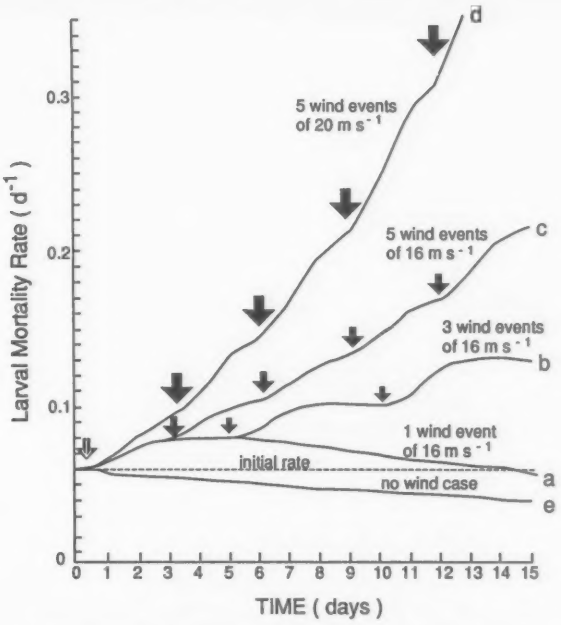

FIGURE 3.—Mortality rate predicted for larval northern anchovy positioned at 3 m depth in the water column (the depth of maximum growth and survival in the model water column). Curve a shows the predicted mortality rate for an event where the wind blows at 16 m s^{-1} for 24 hours. Curves b, c, and d show the mortality rate for larvae experiencing multiple wind events. Curve e gives the mortality rate where winds are calm during the simulated 15 d period. Day zero is the day of first feeding of a cohort of larvae. Arrows indicate the beginning of wind events.

The mortality rate also increases with the strength of the storms. For larvae enduring 5 wind events of 20 m s^{-1} wind speed, each lasting 24 hours, the mortality rate at day 13 is 35% d^{-1} and 45% at day 15 (curve d in Figure 3). Five storms of this magnitude occurring within a 2 wk period are not likely. However, our predicted mortality rates of between 10 and 20% d^{-1} for more common wind conditions (Fig. 4) are in the same range as rates calculated from field data (see figure 1 of Peterman and Bradford 1987).

Food Limiting Conditions

The next model experimentation was conducted to determine the circumstances under which wind events might prove beneficial. Up to this point we have assumed that initial prey concentrations near the surface are sufficient to support optimal growth of northern anchovy larvae before any wind mixing disperses these concentrations. As we have seen above, under these circumstances, all wind events are detrimental to developing larvae. However, we shall now demonstrate that if initial food levels are not sufficient for rapid growth of larvae, a storm may actually enhance the survival of larvae emerging from the yolk-sac stage after the storm.

The initial condition profiles of phytoplankton, zooplankton, and nutrients for the case of insufficient, prestorm prey concentrations are shown in Figure 5a. Notice that the concentration of zooplankton near the surface is only 2.7 μg atom N ℓ^{-1} where the initial concentration of zooplankton in the previous simulations was 3.7 μg atom N ℓ^{-1}. As before, it is assumed that only 25% of this total zooplankton biomass is suitable as food for larval anchovy (estimated from data of Mullin et al. 1985). With this food limiting condition, the growth rate of northern anchovy larvae feeding near the surface is only 15% d^{-1}. The mortality rate of the larvae

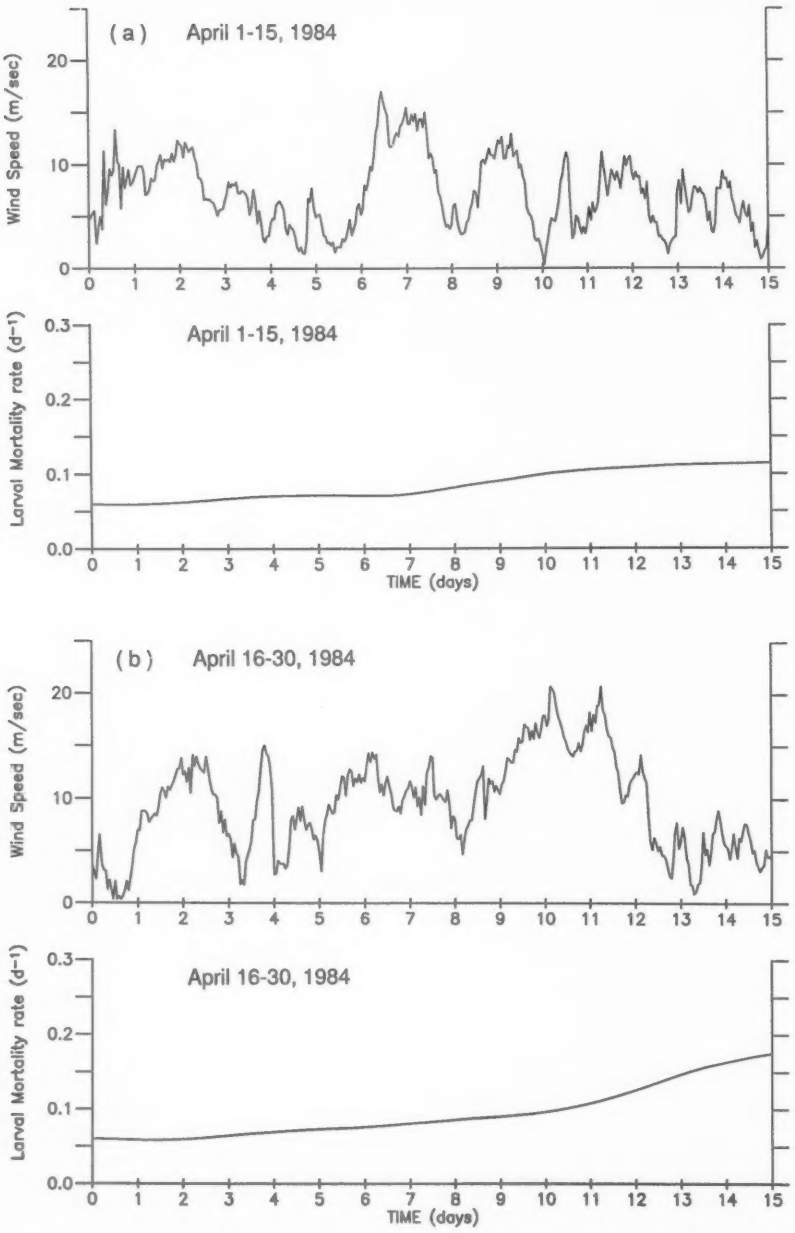

FIGURE 4.—Larva mortality rate of the northern anchovy predicted by the model using wind data from April 1984 recorded by NDBO (National Data Buoy Office, NOAA) mooring 46012 located at lat. 37.4°N, long. 122.7°W. The wind record is typical for the southern California coast in spring. (a) The wind speed and larva mortality rate for the period 1–15 April. Day zero is the day of first feeding for larvae emerging from the yolk-sac stage on 1 April. (b) Same as (a) but for the period 16–30 April, with first feeding beginning on 16 April.

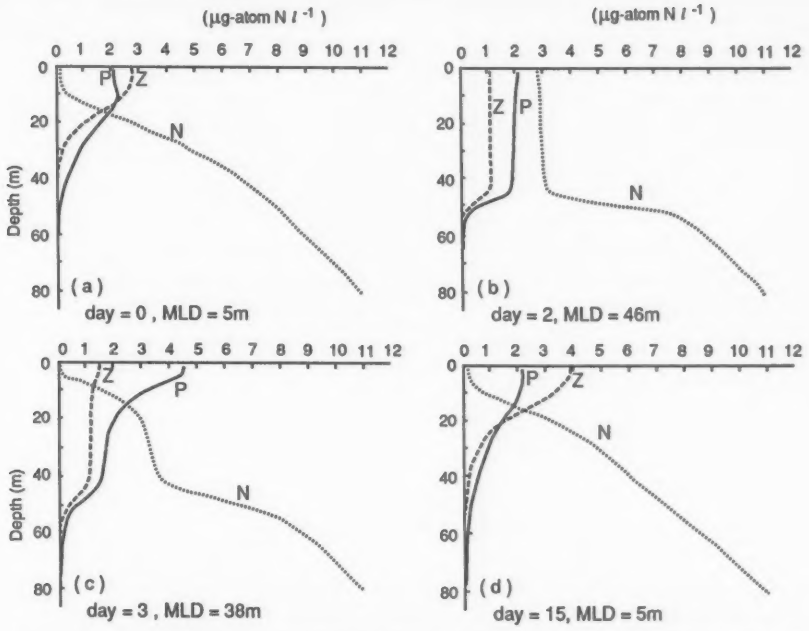

FIGURE 5.—Temporal evolution of the plankton model in response to a wind event of 20 m s^{-1} blowing for 48 hours. The initial conditions shown in (a) are different from those in Figure 1a, as the nitrate concentration continues to increase with depth. This allows more nutrients to be added to the euphotic zone by wind mixing. The initial zooplankton concentration is less than sufficient for optimal growth of northern anchovy larvae.

increases over time even in the absence of any wind event (Fig. 6, curve a).

With these initial conditions, we now determine the influence of a storm with a wind speed of 20 m s^{-1} blowing for 48 hours. The mixed layer deepens to 46 m, entraining nutrients into the euphotic zone while dissipating the existing vertical structure in the upper plankton and nutrient profiles (Fig. 5b). Curve b in Figure 6 shows the decrease in the zooplankton concentration at 3 m depth because of this mixing. However, after the winds cease and turbulence in the water column dissipates, the zooplankton concentration begins to increase. Zooplankton biomass increases as the grazers utilize increased phytoplankton biomass (Fig. 5d). By day 6 (four days after the storm) the zooplankton concentration has surpassed the initial concentration, and by day 8 it has reached concentrations high enough to support optimal growth of anchovy larvae.

However only larvae beginning to feed after the storm truly benefit from poststorm increases in zooplankton biomass. Larvae which existed before and during the storm are adversely affected by the initial decrease in prey concentrations owing to wind mixing. Their growth rate slows and their mortality rate increases to 30% per day by model day 6 (Fig. 6, curve c). But larvae entering the first-feeding stage two days after the storm when zooplankton concentrations are increasing have only a slight initial increase in mortality rate, and then a decrease (Fig. 6, curve d). Larvae emerging from the yolk-sac stage four days after the storm has passed, experience a reduction in mortality even below the initial rate of 6% per day (Fig. 6, curve e) because there is sufficient prey concentrations to support optimal growth.

DISCUSSION

It would appear advantageous for adult northern anchovy to spawn after a storm, so that by the time the eggs hatch and the larvae emerge from the yolk-sac stage, the first-feeding larvae will have high concentrations of prey (induced by the storm) upon which to feed. There is recent evidence that Atlantic menhaden, *Brevoortia tyrannus*, are stimulated to spawn by the pas-

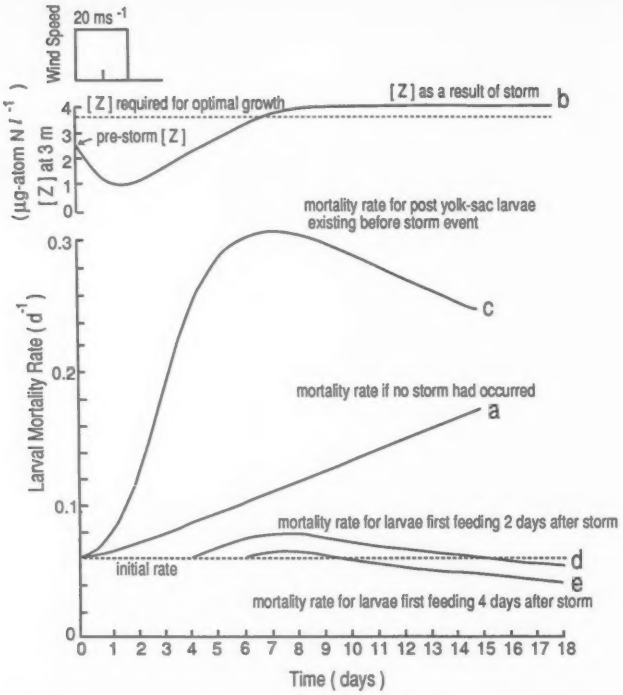
Wind Speed
20 ms -1
[Z] required for optimal growth
[Z] as a result of storm
b
pre-storm [Z]
(µg-atom N l -1)
[Z] at 3 m
mortality rate for post yolk-sac larvae existing before storm event
c
Larval Mortality Rate (d -1)
mortality rate if no storm had occurred
a
mortality rate for larvae first feeding 2 days after storm
initial rate
d
e
mortality rate for larvae first feeding 4 days after storm
Time (days)

FIGURE 6.—Mortality rate predicted for larval northern anchovy positioned at 3 m depth in the simulation shown in Figure 5. Curve a shows the predicted mortality rate where winds are calm during the simulated 15 d period. Mortality rate increases because food is limiting larva growth. Curve b shows the increase in zooplankton biomass at 3 m depth owing to the wind event which entrains nutrients into the euphotic zone. Curve c shows the predicted mortality rate for larvae feeding in the water column during and after the storm. Day zero is the day of first feeding for the cohort of larvae described in curves a and c. Curves d and e show the enhanced survival of larvae first feeding 2 days and 4 days respectively, after passage of the storm.

sage of a storm (Checkley et al. 1988). The strategy of northern anchovy is to spawn continuously (Methot 1981) so that some larvae will be emerging from the yolk-sac stage at just the right time to feed upon high concentrations of microzooplankton induced by a storm.

Since any wind event which falls on the heals of the first beneficial storm will be detrimental, optimal conditions consist of a storm followed by a period of calm during which the larvae can grow into a less vulnerable stage. Any beneficial effect of the first storm will depend on the time required to concentrate new prey biomass. If the first storm is quickly followed by subsequent wind events, the prey will remain disbursed and the first-feeding larvae may not withstand the starvation period. But if the storm is followed by a period of calm winds, turbulence will dissipate, the water column will restratify, and the enhanced secondary production will become concentrated. As the time to complete development from post-yolk-sac stage to this less vulnerable stage is about 15 days (O'Connell 1980), a 2 wk period of calm following a storm strong enough to deepen the mixed layer into the nutricline is theoretically ideal for the survival of the northern anchovy larvae.

These theoretical results may apply as well to other clupeoid species, such as the Atlantic menhaden. Checkley et al. (1988) inferred that the adaptive significance of spawning by *B. tyrannus* during storms derives, in part, from the enhancement of microzooplankton prey for young larvae owing to the storm-induced upwelling. One criterion for maximal survival of the larvae of any clupeoid species would be a close

match between the interstorm duration and the critical development period of the larvae, i.e., the development to a stage where starvation is no longer a major factor.

Survival of northern anchovy larvae in the sea depends on the right type (50–100 μ in size and high nutritional quality) of prey being present in abundance at first feeding (O'Connell and Raymond 1970). Lasker (1975) maintained that the dinoflagellate *Gymnodinium splendens* is small enough to be ingested, has sufficient nutritional qualities, and is abundant enough in subsurface layers to sustain first-feeding anchovy larvae. Lasker regarded microzooplankton as not abundant enough to contribute significantly to larval survival during the first week of life.

Let us assume for the moment that *G. splendens* is the preferred prey of first-feeding anchovy larvae. Let us also assume that this dinoflagellate species is present in the phytoplankton community after a wind event (e.g., as observed by Mullin et al. 1985). The concentration of this motile organism after a wind event depends on its ability to aggregate in the face of turbulent mixing in the water column.

Wroblewski (1984) showed that the vertical diffusivity which just balances the dinoflagellates' ability to aggregate is given by

$$K_v = H W_s$$

where H is the vertical scale of the dinoflagellate layer and W_s is the swimming speed of the dinoflagellate. Cullen and Horrigan (1981) found that if nitrate is available in the upper water column (as after a strong storm), *G. splendens* will migrate to the surface into a layer several meters thick. If the wind event is weak and nitrate is not available in the surface layer, the dinoflagellates will aggregate near the nitracline in a subsurface layer. Assuming H is 5 m and W_s is 1 m h^{-1} (Kiefer and Lasker 1975; Cullen 1985), *G. splendens* should be able to aggregate against a diffusivity of 14×10^{-4} m^2 s^{-1}.

In our model, K_v quickly decays to a background diffusivity of 1×10^{-4} m^2 s^{-1} after cessation of wind forcing (Fig. 2b). Solar heating adds buoyancy at the surface and the turbulent kinetic energy in the mixed layer dissipates through friction. Thus, first-feeding northern anchovy larvae should be able to subsist on layers of *G. splendens* within a day after a storm. The short period of starvation when *G. splendens* are dispersed during the storm should not result in a significant increase in larvae mortality, unless the storm continues for several days. A few days after successful first feeding, the developing anchovy larvae must include microzooplankton in their diet. Our assumption that anchovy larvae feed on microzooplankton is appropriate when simulating larvae mortality over a 15 d period from first feeding.

The concentration of prey required for survival of anchovy larvae is controversial. The laboratory feeding experiment of O'Connell and Raymond (1970) indicated a prey concentration > 800 copepod nauplii ℓ^{-1} were required for maximal survival. More recent laboratory experiments (Houde and Schekter 1981; Munk and Kiorboe 1985) suggest the minimum concentration of prey may be as low as 200 copepod nauplii ℓ^{-1}, but of course the larvae would be expected to grow at a much slower rate (O'Connell and Raymond 1970).

Even concentrations of 200 nauplii ℓ^{-1} are high compared to estimates of *average* densities of microzooplankton in the sea (Beers and Steward 1967). However, as pointed out by Owen (1989), maximal concentration of prey rather than average concentration (estimated from integrating net hauls or pump samples) is the relevant quantity.

The highest zooplankton concentration in the model (at 3 m depth in Figure 1a) is about 4 μg atom N ℓ^{-1} of which 25% or 1 μg atom N ℓ^{-1} is larval anchovy food (e.g., copepod nauplii). This is equivalent to about 14 μg N ℓ^{-1} of copepod nauplii. The nitrogen content of *Paracalanus* stage I nauplii is about 5 ng (Checkley 1980) and of *Calanus* is about 20 ng (Corner et al. 1965; Mullin and Brooks 1967). Thus, 14 μg N ℓ^{-1} of copepod nauplii is equivalent to 2,800 *Paracalanus* stage I nauplii ℓ^{-1} or 700 *Calanus* stage I nauplii ℓ^{-1}. These concentrations correspond roughly to the prey densities used experimentally by O'Connell and Raymond 1970), but are two orders of magnitude higher than the median numbers m^{-3} observed in pump samples from the sea taken by Mullin et al. (1985) before and after a storm.

The overestimation of zooplankton biomass in the model is due to the omission of vertical loss processes such as sinking of phytoplankton and zooplankton fecal pellets which reduce the total nitrogen available to the plankton ecosystem in the upper water column (Walsh 1983; Checkley 1985). However, we would get the same response in the mortality of larval anchovy presented above, if we altered the model to simulate more realistic zooplankton concentrations, while

also reducing the concentration of prey required for the baseline growth rate of the anchovy larvae. The crux of the model is the lowering of prey concentration due to wind mixing, a corresponding decrease in ingestion and growth rate of anchovy larvae, and an increase over time of the larval mortality rate with suppressed growth.

Owen (1989) showed that microzooplankton do occur in concentrations greater than 100 organisms ℓ^{-1} on the microscale (centimeters) in patches of fine scale (meter) size. Owen found that concentrations of organisms within the patches were greater at low wind speeds. Motile organisms showed higher patch concentrations than would be expected solely from reproduction of the organisms. Rothschild and Osborne (1988) discovered mathematically that a beneficial effect of moderate turbulence is to increase the encounter rate of prey and predator on these microscales. These recent observations and theory emphasize the need to examine the feeding and survival of larval northern anchovy on microscale and fine scales. Our model with a 2.5 m vertical grid spacing does not resolve biological and physical processes on these scales. Future modeling research should compare the beneficial (e.g., productivity enhancement) and detrimental (e.g., prey dispersion) effects of storm-induced mixing on the microscale feeding environment of larval anchovy (see Vlymen 1977; Lasker and Zweifel 1978).

We conclude that wind conditions during the spawning period which are optimal for the survival of northern anchovy larvae encompass 1) wind speeds high enough (>10 m s^{-1}, depending on the water column stratification) to deepen the mixed layer into the nutricline; 2) wind event durations long enough (greater than half an inertial period, or about 8 hours at lat. 35°N) to maximally deepen the mixed layer, but short enough to maximize calm periods between storms; and 3) wind event frequency low enough (one major storm every two weeks) to allow development of larvae to a stage where carbohydrate, protein, and lipid reserves can mitigate subsequent starvation periods (about 15 days of development, depending on water column temperature).

Our conclusions are supported by the observation that northern anchovy populations off central and southern California spawn during the winter and spring months, when wind conditions can be optimal by our theoretical calculations. They do not spawn during the summer when winds are most calm and the water column is highly stratified, as one would expect considering Lasker's hypothesis alone.

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Precision and Bias of Estimates of Larval Mortality

Nancy C. H. Lo, John R. Hunter, and Roger P. Hewitt

ABSTRACT: The results of four ichthyoplankton surveys conducted during January through April 1984 off the coast of California were used as the basis for Monte Carlo simulation of populations of northern anchovy, *Engraulis mordax*, larvae. The simulated populations were sampled and larval mortality rate was calculated, using established analytical procedures. Results may be used to determine the precision of an estimate of larval mortality rate and to determine the number of plankton tows required to detect a difference in mortality rates between two surveys. The estimated mortality rate was found to be biased high when the larval growth rate is overestimated and biased low when the growth rate is underestimated. The bias is asymmetrically distributed and greatest when the assumed growth substantially overestimates the real growth. The results justify interannual comparisons of larval anchovy mortality rates when interannual variation in larval growth is less than twofold. The results also indicate that the sample size required for adequate precision of estimates of mortality rates is modest compared to that required for adequate representation of the spawning season and larval habitat.

The early life stages of several fish have been extensively studied as they are the link between the present adult stock and some future recruitment to the adult stock. Frustrated with the apparent lack of a clear relationship between stock and recruitment, fishery scientists have focused attention on events during the larval stage and their ultimate effect on survival to the juvenile and adult stages. Several hypotheses have been proposed (e.g., Hjort 1913); however, an understanding of the precision and accuracy of estimates of larval mortality rates is necessary to distinguish among them (Gulland 1971). This paper draws upon our experience with the northern anchovy, *Engraulis mordax*, to address this issue.

We focus on three questions: 1) What is the minimum number of plankton tows required to estimate the mortality rate of young larvae (<20 days old) for a given coefficient of variation? 2) What is the minimum number of plankton tows required to detect a difference in the mortality rates of young larvae between two surveys? 3) How does violation of the assumption of a constant growth model affect the estimate of larval mortality?

Several biases associated with sampling northern anchovy larvae have been identified and quantified. Pelagic ichthyoplankton are caught by lowering a fine-mesh net to a depth below the larval habitat and by steadily retrieving it to the surface of the ocean (Smith and Richardson 1977). Variability in the volume of water filtered per unit of depth affects the number of larvae captured; Ahlstrom (1948) formulated the "standard haul factor" to adjust for this bias. Larvae are extruded through the meshes of the sampling gear: retention rates can be expressed as a function of larval length and mesh size (Lenarz 1972; Zweifel and Smith 1981; Lo 1983). Larvae also evade capture as evidenced by differences in the night and day catch rates (Ahlstrom 1954; Smith 1981): retention rates can be expressed as a function of larval length and the diurnal time of capture (Hewitt and Methot 1982). The apparent length of larvae is affected by abrasion from the sampling net and by the preservative solution: live larval length may be expressed as a function of preserved larval length and the duration of the plankton tow (Theilacker 1980).

The application of these corrections yields unbiased estimates of the density of larvae in each of several length categories. Age-specific variations in growth introduce variability in the duration of time that a larva of given length is vulnerable to capture. The density of larvae divided by the duration of growth through each length category yields estimates of the number of larvae of a given age produced per unit sea-surface-area per unit time, which is termed larval production (Hewitt and Methot 1982). Yolk-sac larvae growth has been described as a function of temperature (Zweifel and Lasker

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1976; Lo 1983). Growth of feeding larvae has been described as a function of season (Methot and Hewitt 1980[1]). Interannual variations in growth have not been described, and in the absence of additional information, a larval growth model with constant coefficients is used for all years. The set of coefficients encompassed temperature effects as well as seasonal effects. The rate of decline of larval production with age represents the mortality rate (Hewitt 1981).

In actual practice, a negative binomial-weighted model (Bissel 1972) has been employed to convert length-specific distributions of larval density to unbiased age-specific distributions of larval production, assuming one set of size-specific extrusion and voidance rates (Zweifel and Smith 1981; Hewitt 1982; Hewitt and Methot 1982; Hewitt and Brewer 1983; Picquelle and Hewitt 1983, 1984; Lo 1985). The negative binomial distribution is recommended for describing sample counts of fish eggs and larvae (Smith and Richardson 1977); the distribution is capable of adequately describing patchy spatial distribution patterns. The arithmetic means of these distributions describe the mortality (or production) of larvae with age.

Although the negative binomial-weighted model produces an estimate of the variance of the mean density at a particular age, each age-specific distribution is unique because of the spatial dispersal of the larvae (Hewitt 1981). The variance of the mean density is underestimated as the extrusion and avoidance are assumed to be constant, and the variance about the mortality curve (hence, the variance of the mortality rate) is not easily determined. In the simulation, random variation of avoidance of the net and extrusion through the meshes of the net were included so that the variance of the mortality rate might best be evaluated. The approach used here is to construct a simulated population, sample it with simulated surveys, and estimate the mortality rate of larvae, using the procedures described above. By conducting many surveys, the accuracy and precision of the estimates of mortality rates may be investigated.

Potential biases in estimating larval mortality, introduced by assuming no interannual variation in growth, were our main concern and were investigated by simulation. Growth rates were varied when constructing the populations; mortality rates were subsequently calculated assuming a set of growth rates (i.e., no interannual variation). By comparing the calculated mortality rates to a known rate, the magnitude of biases may be investigated.

METHODS

A Monte Carlo simulation model (Fig. 1) was employed to address the questions pertaining to the biases and precision of the estimate of larval mortality. A population of anchovy larvae was constructed using observed seasonal and geographic distributions. A known mortality rate was imposed on the population and sampling effort was varied over time and space. Known sampling biases were imposed and then adjusted for using the same techniques for calculating larval mortality rate as have been used on real surveys. Several hundred simulated surveys were conducted to assess the accuracy and precision of the estimates of mortality rates. Simulated larval growth was also varied to determine the sensitivity of the estimates of mortality rates to an assumption of constant larval growth. The details of this simulation are outlined in the following paragraphs.

Larval Population

A series of CalCOFI[2] ichthyoplankton cruises conducted in 1984 (Fig. 2) was used as a basis for constructing the population of larvae in the ocean. The total abundance of anchovy larvae at each station was adjusted for extrusion of small larvae through the meshes of the net (Fig. 3) and avoidance of the net by large larvae (Fig. 4). The adjusted catches were then stratified by geographic region (Fig. 2), month, and temperature. The negative binomial distribution was fit to the observations (positive tows only) in each region-month-temperature cell owing to the patchiness of larvae and the fact that the mean larval abundance is less than the standard deviation in general (Table 1). Samples were randomly drawn from these distributions (where the variate was the total number of larvae <9.25 mm per station) to conduct a simulated survey.

[1]Methot, R. D., Jr., and R. P. Hewitt. 1980. A generalized growth curve for young anchovy larvae: derivation and tabular example. SWFC Admin. Rep. LJ-80-17, 8 p.

[2]California Cooperative Oceanic Fisheries Investigations (CalCOFI) is a consortium of marine institutions engaged in long-term monitoring and study of the pelagic ecology of the California Current. Large-scale ichthyoplankton surveys have been conducted since 1949. See Hewitt 1988, Reid 1988, and Smith and Moser 1988 for reviews.

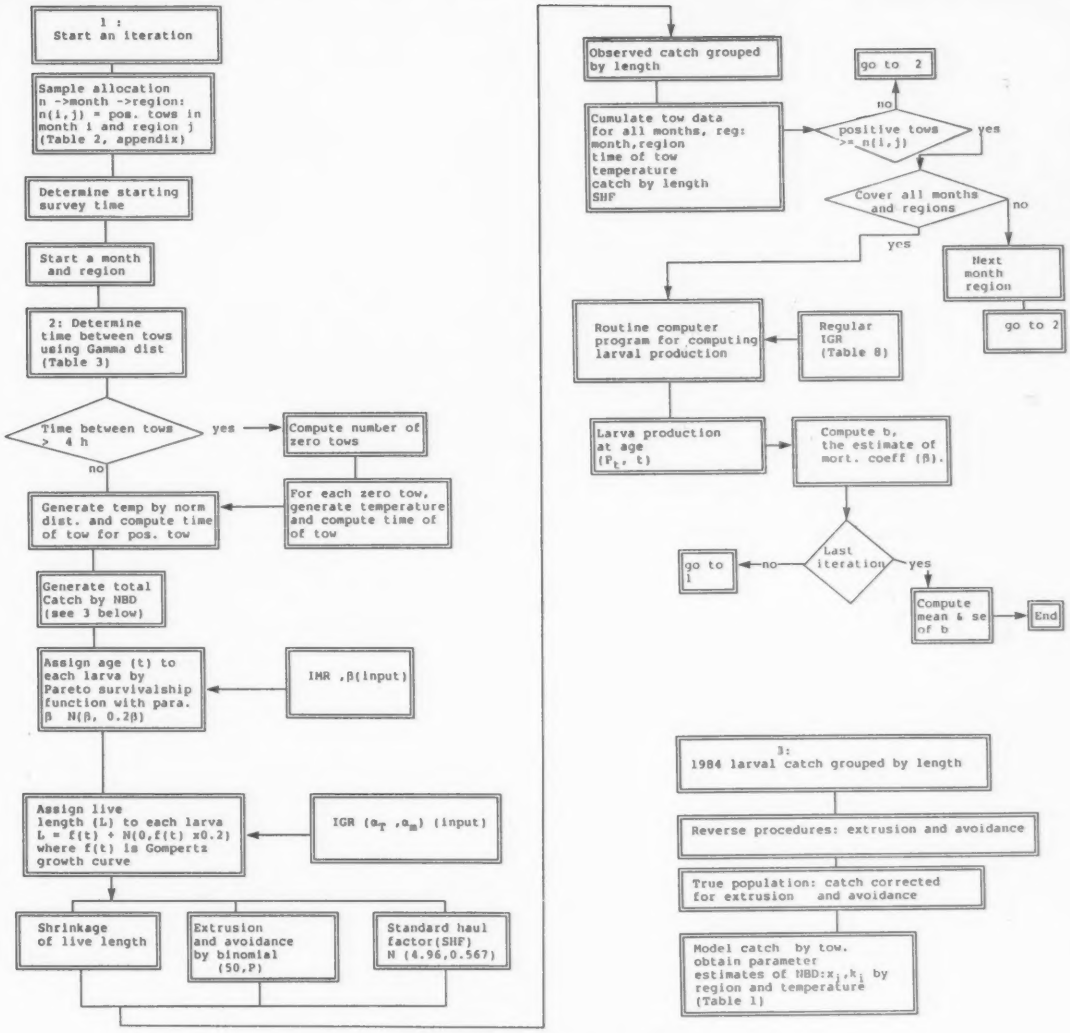


FIGURE 1.—Flow chart of the simulation.

Allocation of Sampling Effort

Simulated population encountered by plankton tows was computed according to their distribution in 1984 by month and region (Table 1). The portion of simulated tows that contained anchovy larvae was similarly determined (Table 2; App.). In this way, the sample size (number of tows) could be varied and yet still retain the spatial and temporal distribution of sampling effort that was used in 1984. The time of the simulated tows was assigned by randomly selecting a value from a Gamma distribution fitted to the actual time between tows in each region (Table 3; App.).

Larval Mortality Rate

Because it was found that anchovy larvae suffer higher mortality during the first-feeding period than during later stages, a Pareto function describes the survival of anchovy larvae younger than 20 days adequately (Hewitt and Brewer 1983; Lo 1985, 1986). In the present study, we used the Pareto function to assign age to the larvae in the population (Table 1; Fig. 5; App.).

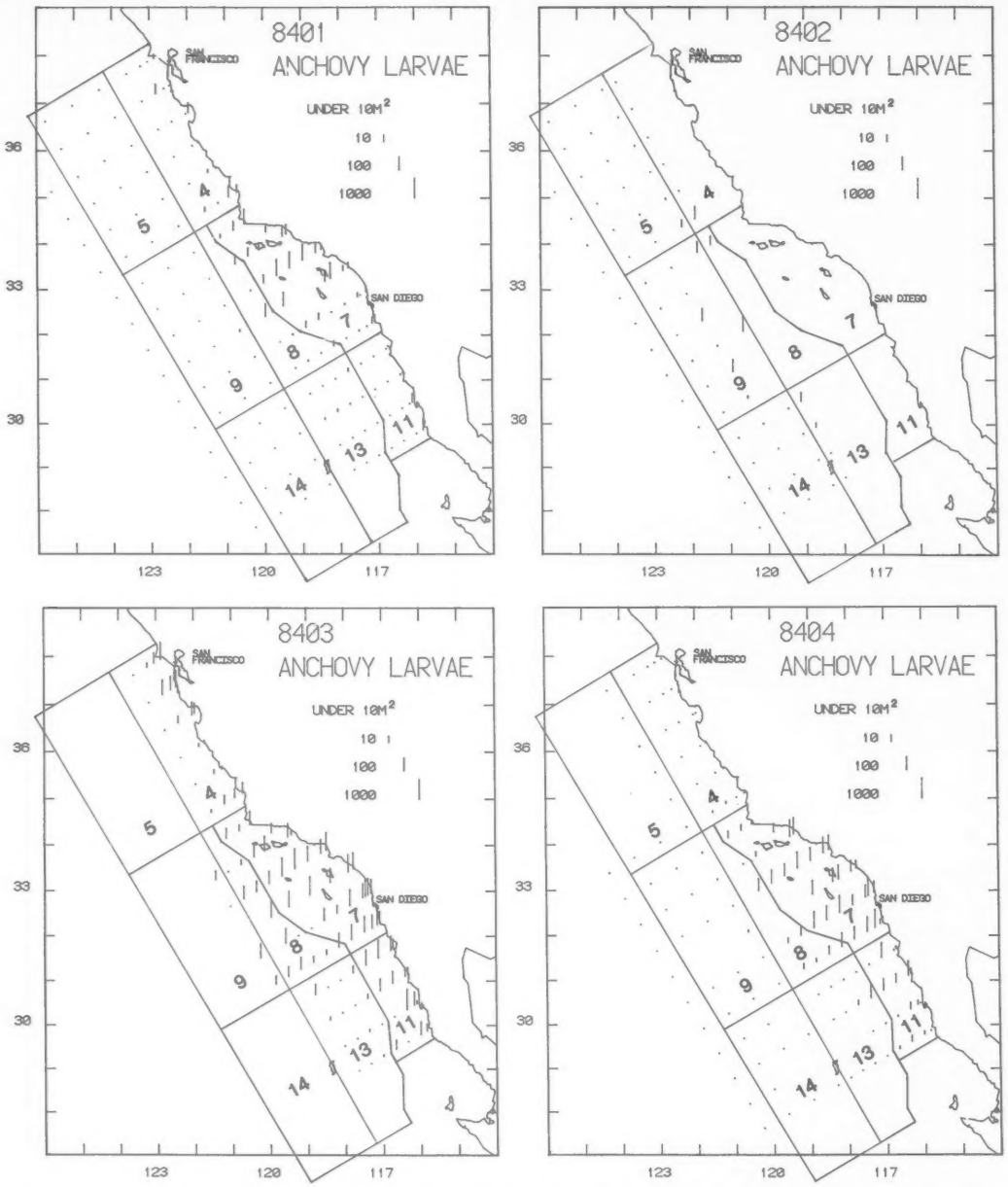


FIGURE 2.—Description of the seasonal and geographic distribution of sampling effort on a series of ichthyoplankton cruises conducted off the coast of California in 1984. The abundance of anchovy larvae at each station is indicated by the height of the "tree." Stations are grouped into geographic regions 4 through 14.

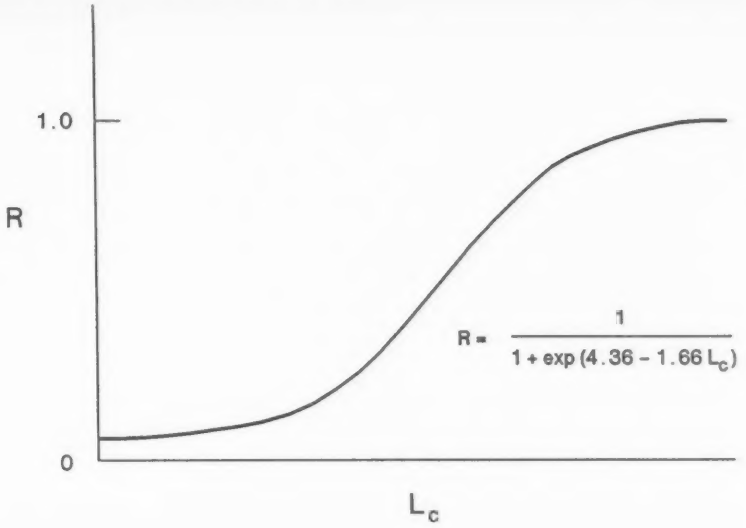
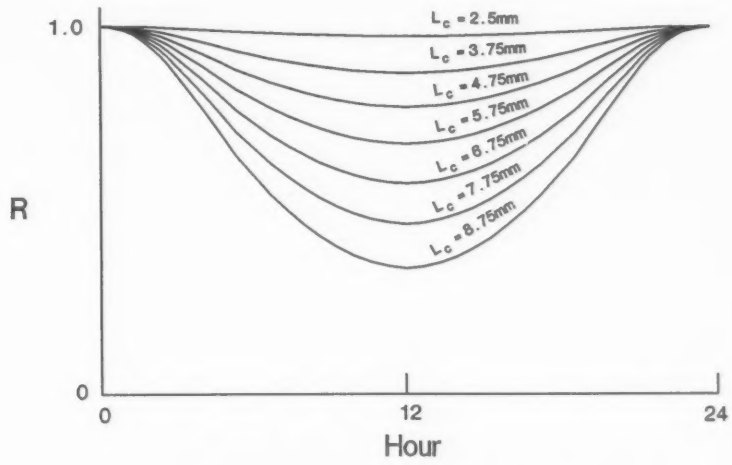


FIGURE 3.—Retention of anchovy larvae not extruded through the meshes of a plankton net constructed of 0.505 mm nylon (Lo 1983). R is the portion of larvae, of preserved length L_c, retained in the net.



$$R = \left(\frac{1 + DN_L}{2}\right) + \left(\frac{1 - DN_L}{2}\right) \cos\left(\frac{2\pi * Hour}{24}\right)$$

where:

L_c	DN_L
2.5	1.67
3.75	1.47
4.75	1.46
5.75	1.27
6.75	1.21
7.75	1.16
8.75	1.13

FIGURE 4.—Retention of anchovy larvae which have not avoided capture (Hewitt and Methot 1982). R is the portion of larvae, of preserved length L_c, retained in the net. DN_L is the length-specific day/night catch ratio.

TABLE 1.—Simulated population of anchovy larvae based on a series of ichthyoplankton surveys conducted in 1984. Tabulated values are the parameters (m and k) of negative binomial distributions[1] fit to the population stratified by month, region, and temperature.

		Temperature °C							
		≤13°		13.1°–14°		14.1°–15°		>15°	
Month	Region	m	k	m	k	m	k	m	k
1	4	31.25	0.39	63.00	0.34	27.50	0.51	27.50	0.51
	5	[2]0.25	∞	0.25	∞	0.25	∞	0.25	∞
	7	270.50	0.62	270.50	0.62	147.08	0.25	619.10	0.14
	8	2.00	∞	2.00	0.31	44.00	0.22	98.60	0.22
	9	34.00	0.60	34.00	0.60	136.00	0.41	51.00	4.33
	11	56.80	0.55	56.80	0.55	56.80	0.55	56.80	0.55
	13	6.80	0.37	6.80	0.37	6.80	0.37	6.80	0.37
	14	0.25	∞	0.25	∞	0.25	∞	0.25	∞
2	4	558.17	0.64	120.50	0.32	22.50	0.97	22.50	0.97
	5	0.25	∞	0.25	∞	0.25	∞	0.25	∞
	7	270.50	0.62	270.50	0.62	147.08	0.25	619.10	0.14
	8	2.00	∞	2.00	0.31	44.00	0.22	98.60	0.22
	9	34.00	0.60	34.00	0.60	136.00	0.41	51.00	4.33
	11	56.80	0.55	56.80	0.55	56.80	0.55	56.80	0.55
	13	6.80	0.37	6.80	0.37	6.80	0.37	6.80	0.37
	14	0.25	∞	0.25	∞	0.25	∞	0.25	∞
3	4	2.00	0.40	2.00	0.40	2.00	0.40	2.00	0.40
	5	0.25	∞	0.25	∞	0.25	∞	0.25	∞
	7	4.00	5.39	7.33	5.39	522.33	1.07	790.60	1.38
	8	117.50	0.50	117.50	0.50	520.00	0.20	206.30	0.45
	9	0.00	0.00	0.00	0.00	150.50	0.78	150.50	0.78
	11	14.50	2.14	14.50	2.14	147.00	1.22	514.30	0.45
	13	6.80	0.37	6.80	0.37	6.80	0.37	6.80	0.37
	14	0.25	∞	0.25	∞	0.25	∞	0.25	∞
	4	2.00	0.40	2.00	0.40	2.00	0.40	2.00	0.40
	5	0.25	∞	0.25	∞	0.25	∞	0.25	∞
	7	4.00	5.39	7.33	5.39	522.33	1.07	790.60	1.38
	8	117.50	0.50	117.50	0.50	520.00	0.20	206.30	0.45
	9	0.00	0.00	0.00	0.00	150.50	0.78	150.50	0.78
	11	14.50	2.14	14.50	2.14	147.00	1.22	514.30	0.45
	13	6.80	0.37	6.80	0.37	6.80	0.37	6.80	0.37
	14	0.25	∞	0.25	∞	0.25	∞	0.25	∞

[1]Negative binomial distribution where

$$P(X = x) = \frac{(x + k - 1)!}{x!(k - 1)!} * [m/m + k)]^x * [k/m + k)]^k \text{ for } x = 0,1,2,3,....$$

[2]Poisson distribution was used where $P(X = x) = (m^x e^{-m})/x!$ for $x = 0,1,2,3,....$

A two-step Gompertz growth curve (Fig. 6) was used to determine the corresponding larval length. The length at age was generated based on a normal distribution with mean equal to the length computed from the Gompertz growth curve and a standard deviation equal to 0.2 times the length. (The standard deviation is normally proportional to the mean length at age.) The coefficient of variation of 0.2 was arbitrarily chosen because no direct estimate of the standard deviation was available. These simulated larvae, with assigned ages and lengths, composed the catches.

Sampling Biases

The simulated catches were reduced to account for the effects of extrusion and avoidance.

TABLE 2.—Distribution of sampling effort during January through April 1984 by region and month, where $p(i)$ is the *proportion of tows for month i* and $\Sigma p(i) = 1$, $g(j|i)$ is the proportion of tows made in region j during month i and $\Sigma q(j|i) = 1$, and $r(j|i)$ is the proportion of positive tows for region j during month i and $0 \leq f(j|i) \leq 1$. The number of tows is indicated by N, and the positive tows are indicated by n (i.e., those tows which contained anchovy larvae)

	January		February		March		April		Total
i =	1		2		3		4		
N =	139		89		67		54		349
n =	55		55		47		19		176
$p(i)$	0.40		0.26		0.19		0.15		0.50
Region	q	r	q	r	q	r	q	r	
4	0.14	0.43	0.28	0.29	0	—	0.36	0.14	
5	0.14	0.06	0.20	0.06	0	—	0.15	0	
7	0.25	0.90	0.21	1.00	0.26	0.94	0.26	0.93	
8	0.04	0.67	0.01	1.00	0.14	0.88	0.02	1.00	
9	0.13	0.06	0.16	0.63	0.02	1.00	0.16	0.11	
11	0.14	0.33	0.06	0	0.24	0.88	0.05	0	
13	0.09	0.27	0.02	1.00	0.25	0.41	0	—	
14	0.07	0.08	0.06	0.17	0.09	0	0	—	
	1.00		1.00		1.00		1.00		

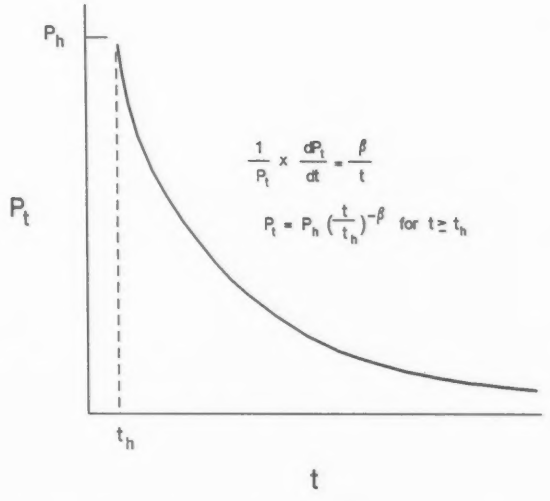


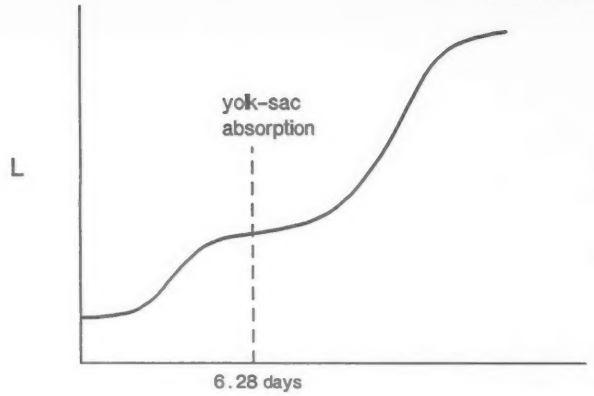
FIGURE 5.—Pareto model of larval production where larval mortality is assumed to decline with increasing age (Lo 1985 and 1986). P_t is the daily production of larvae at age t; β is the mortality coefficient; and t_h is the age at hatch.

TABLE 3.—Two parameters describing Gamma distributions[1] fit to the time between tows minus the constant in each region. Each of these distributions is shifted by the addition of the constant listed. The constant is the minimum time (hours) between two positive tows.

Regional	α	β	Constant
4	0.275	43.71	2
5	0.510	3.92	4
7	0.291	34.93	2
8	0.346	42.19	3
9	0.838	39.47	4
11	0.714	5.03	2
13	0.561	21.08	3
14	0.500	69.00	4

[1]Gamma distribution where

$$g(x) = \frac{1}{\beta(\alpha - 1)!} (x/\beta)^{-(\alpha-1)} \exp(-x/\beta) \text{ for } x > 0.$$



$$L = 4.25 \left(\frac{0.32}{4.25}\right)^{e^{-\alpha_T t}} \text{ for } t \leq 6.28 \text{ days}$$

$$L = 27 \left(\frac{4.1}{27}\right)^{e^{-\alpha_m t}} \text{ for } t > 6.28 \text{ days}$$

Where: $\alpha_T = a_T \exp(b_T \times \text{TEMPERATURE})$

$= 0.11 \exp(0.12 \times \text{TEMPERATURE})$

$\alpha_m = (a_m - b_m \times \text{MONTH})^{-1}$

$= (22.48 - 0.83 \times \text{MONTH})^{-1}$

FIGURE 6.—Temperature-dependent and season-dependent larval growth curves (Methot and Hewitt 1980; Lo 1983). Gompertz models are used to describe each growth phase where α_T is the temperature-dependent growth coefficient and α_m is the season-dependent growth coefficient.

The fraction, p, of larvae extruded through the mesh or avoiding the net was generated by a sample mean of a binomial random variable, y, with parameters N and P. The parameter: N was set to 50 and P was the length-specific extrusion rate or avoidance rate from the same equations used to construct the population from the 1984 surveys. Thus p equaled $y/50$. Although p has a mean of P, it was not necessarily equal to P for each simulation run. The live lengths of larvae were reduced to account for the effects of net abrasion and preservaton effects (Theilacker 1980; Fig. 7). A standard haul factor was selected from the observed normal distribution of this variate (mean = 4.96, SD = 0.567) and used to index the volume of water filtered per unit of depth sampled. These catches then formed the raw material for the mortality estimation procedure.

Estimating Mortality Rate

The larvae in each catch were grouped into 1 mm length categories. A weighted negative binomial distribution was fitted to each length category where the original variate was the number of larvae (of a given length category) per station. Using this procedure, each observation was weighted for the effects of sampling biases (extrusion, avoidance, volume of water filtered, growth and shrinkage). The final variate was the number of larvae (of a given age) produced per day per 0.05 m^2 of sea surface. The rate at which larval production declines with time was defined as the mortality rate. For the Pareto model, the mortality rate was assumed to decline with age and mortality was indexed by the mortality coefficient (β). For the simulations described in this report, β was estimated as the slope of the log-

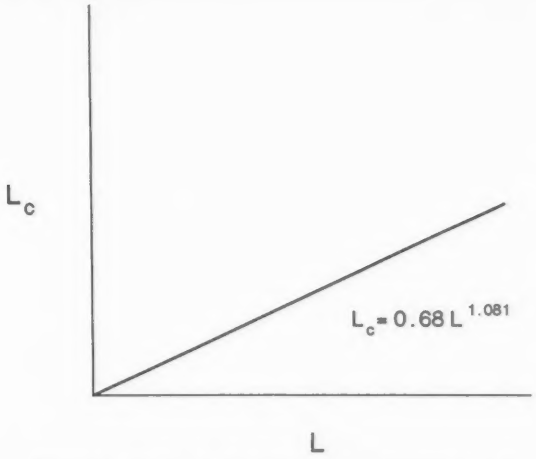


FIGURE 7.—The effect of net abrasion and preservative on the apparent length of anchovy larvae (from Theilacker 1980). L is live larval length; L_c is preserved (captured) larval length, and the length of the plankton tow is 20 minutes.

transformed Pareto function:

$$\ln(P_t) = \ln(P_h) - \beta \ln(t/t_h) .$$

Each simulation that produced an estimate of mortality rate was repeated many times. The collection of estimates of mortality rates was used to assess the accuracy and precision of estimates of mortality rates.

Sample Size for Detecting a Difference of Mortality Rates

The minimum sample size required to detect a difference between two mortalities was computed by two methods.

The *CV* Method

The coefficient of variation (cv) of the estimate of the difference between two mortality coefficients ($D = \beta_2 - \beta_1$) was calculated by

$$cv(d) = \frac{[\mathrm{var}(b_1) + \mathrm{var}(b_2)]^{0.5}}{D} \quad \text{for } D \neq 0 \qquad (1)$$

where d is the estimate of D, the difference between mortality coefficients β_1 and $\beta_2 (D = \beta_2 - \beta_1)$; b_1 and b_2 are the estimates of β_1 and β_2; $\mathrm{var}(b_1)$ and $\mathrm{var}(b_2)$ varying with sample size are computed in the simulation. The relationship between the sample size (n) and two elements, $cv(d)$ and D, enables us to determine the minimum sample size for a given $cv(d)$ and D.

The Power Method

The probability of detecting a difference in two mortality rates, given that there is a difference, was calculated as

$$P[d > c(\beta_1,n) \mid D] = P[Z > z(\beta_1,\beta_2,n)] \qquad (2)$$

where d follows a normal distribution with a mean of D and a variance of $[\mathrm{SE}(d)]^2$; Z follows a normal distribution with a mean of 0 and a variance of 1:

$$c(\beta_1,n) = 2\,\mathrm{SE}(d) = 2\sqrt{2}\,\mathrm{SE}(b) \quad \text{for } \beta_1 = \beta_2 (D = 0) \qquad (3)$$

$$z(\beta_1,\beta_2,n) = \frac{c(\beta_1,n) - D}{\mathrm{SE}(d)}$$

$$\text{and } \mathrm{SE}(d) = [\mathrm{var}(b_1) + \mathrm{var}(b_2)]^{0.5} \quad \text{for } \beta_2 \neq \beta_1 (D \neq 0).$$

A normal distribution table was used to obtain the probability values.

Relationship Between Growth and Mortality

The mortality coefficient (β) was fixed. Five

populations were constructed with data from a single region-month stratum using five combinations of growth coefficients for yolk-sac (α_T, a temperature-specific coefficient) and feeding larvae (α_m, a season-specific coefficient) (see Table 8). Each population was sampled repeatedly and an average mortality coefficient calculated assuming standard growth coefficients. These mortality coefficients were then compared with the fixed mortality coefficient used to construct the populations.

RESULTS

The simulation model was used to estimate the following: 1) the mortality coefficients and their standard errors for various sample sizes when the true mortality coefficient was fixed, 2) the difference between two mortality coefficients and its standard error for various sample sizes, and 3) the mortality coefficients, assuming various growth rates.

Estimates of β with Various Sample Sizes

The mortality coefficient (β) was fixed at 1.5 for the inshore area (regions 4, 7, 8, 11, and 13; Fig. 2) and at 0.05 for the offshore area (regions 5, 9, and 14). The lower coefficient was required to generate simulated catch curves similar to those observed in offshore areas. The low mortality coefficient observed in offshore areas was likely the result of transport of older larvae from inshore to offshore regions (Power 1986). The average mortality coefficient (β), weighted by area of each region, was 1.41.

For each sample size (50, 100, 200, 300, and 400 plankton tows) 100 computer runs were made, and an estimate of the mortality coefficient (b) was calculated. The mean mortality coefficient, its standard error, and the coefficient of variation (cv) are listed in Table 4 for each sample size. The mean mortality coefficient for all sample sizes, except 50, slightly overestimated the true value of $\beta = 1.41$. The cv decreased with increasing sample size.

The relationship between cv and the number of positive tows (n) was quantified by assuming that half of the tows contained anchovy larvae (the actual portion of positive tows in 1984 was 0.5) (Table 2).The curve (Fig. 8) may be described by the power function:

$$cv(b) = 0.418\, n^{-0.47}$$

From Figure 8 and the above expression, cv may be expected to be 0.10, 0.06, or 0.05 for 20, 60, or 100 positive tows. For $n > 100$, cv may be expected to decrease at a slow rate. Thus a survey of 120 tows, yielding 60 positive tows, is sufficient to estimate the mortality coefficient with an expected $cv = 0.06$. Data from annual surveys conducted between 1980 and 1987, where the portion of positive tows ranged from 0.47 to 0.98, are also shown on Figure 8. The variation of b, as related to sample size during 1980–87, follows the relationship estimated from a single year's data and implies that the relationship can be used as a guide for sample size determination.

TABLE 4.—Mean, standard error (SE), and coefficient of variation (cv) of estimates of the mortality coefficient (b) for various sample sizes (N), with 50% positive for anchovy larvae (n = 0.5 N), from 100 computer runs of each simulated survey.

N	n	mean	SE	cv = SE/mean
50	25	1.39	0.13	0.09
100	50	1.43	0.09	0.06
200	100	1.44	0.06	0.04
300	150	1.44	0.06	0.05
400	200	1.43	0.05	0.03

Estimates of *D* with Various Sample Sizes

The mortality coefficient (β) was fixed at 1.0, 1.5, 2.0, 2.5, and 3.0 for the inshore area (regions 4, 7, 8, 11, and 13). The inshore area was relatively well sampled and contained relatively high abundances of larvae; the proportion of positive stations in these regions was approximately 0.6 (Tables 1, 2). Estimated mortality coefficients (b) were determined for five simulated populations (corresponding to each of the five mortality coefficients (β)) using sample sizes of 50, 100, and 200 plankton tows with 60% of them positive for anchovy larvae.

The average estimated mortality coefficient and its standard error were determined after 100 computer runs and listed in Table 5. As expected, standard errors decreased with increased sample size. The estimated mortality coefficient was biased slightly low for $\beta < 2$ and biased slightly high for $\beta > 2$. The biases are negligible although they appeared to increase in magnitude as β departed from 2. The estimates of mortality rates and their standard errors were used to determine minimum sample size by two methods.

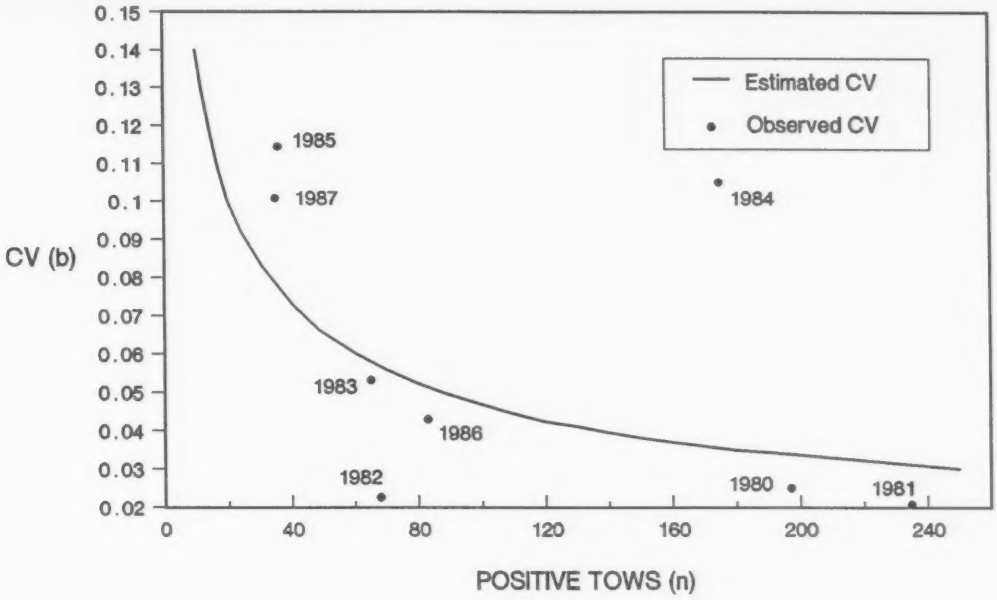


FIGURE 8.—The relationship between the coefficient of variation, cv(b), and the number of positive tows, n, derived from the results of the simulation. 1980–87 survey results are also plotted.

The *CV* Method

The *cv* of the estimate of the difference between two mortality coefficients, *cv*(*d*) (Equation (1)), was calculated for various mortality differences and sample sizes using the data listed in Table 5. The *cv*(*d*) decreases linearly with the difference between mortality coefficients (*D*), increases linearly with the absolute value of the larger of the two mortality coefficients (β_2), and exponentially declines with increasing sample size (*N*, *n*) (Table 6). The required sample size was thus estimated by regressing the number of positive tows on β_2, *D*, and ln[*cv*(*d*)]:

$$n = -101 + 24.8\,\beta_2 - 150\,D - 128\,\ln[cv(d)]\,.$$

For example, estimating the difference between two estimated mortality coefficients, when the true mortality coefficients are 3.0 and

TABLE 5.—Mean and standard error (SE) of estimated mortality coefficient based on 100 computer runs. Five populations were simulated, each with a different mortality coefficient (β). Simulated surveys used three sample sizes (*N*) with 60% of the plankton tows positive for anchovy larvae (*n*).

	Sample size *N*(*n*)					
β	50(30)		100(60)		200(120)	
	mean	SE	mean	SE	mean	SE
1.00	0.90	0.100	0.91	0.075	0.93	0.058
1.50	1.44	0.090	1.44	0.064	1.44	0.060
2.00	1.98	0.120	1.99	0.087	2.01	0.058
2.50	2.56	0.110	2.57	0.097	2.58	0.065
3.00	3.18	0.170	3.18	0.100	3.18	0.075

TABLE 6.—Coefficient of variation of the estimate of the difference between two mortality coefficients, *cv*(*d*), calculated for various mortality differences, *D*, and sample sizes, *n*. The number of positive tows, *n*, was 60% of the total number of tows.

	Sample size *N*(*n*)		
$\beta_2 - \beta_1$	50(30)	100(60)	200(120)
D = 0.5			
1.5 − 1.0	0.268	0.196	0.166
2.0 − 1.5	0.300	0.210	0.166
2.5 − 2.0	0.320	0.260	0.170
3.0 − 2.5	0.400	0.270	0.190
D = 1.0			
2.0 − 1.0	0.156	0.115	0.082
2.5 − 1.5	0.142	0.116	0.088
3.0 − 2.0	0.208	0.133	0.095
D = 1.5			
2.5 − 1.0	0.100	0.082	0.058
3.0 − 1.5	0.130	0.079	0.064

2.0 ($\beta_1 = 2.0$, $\beta_2 = 3.0$, $D = 1.0$), with a $cv(d) = 0.15$, will require $n = 67$ positive tows from each population. With 70 positive tows from each population, approximately 95% of the sample differences can be expected to be between 0.70 and 1.30 ($1.0 \pm 2 * 0.15$).

The Power Method

The standard error of the estimated mortality coefficient, SE(b), was modeled as a function of the number of positive tows, n, and the true mortality coefficient (β) using the data listed in Table 5:

$$\mathrm{SE}(b) = 0.356\, n^{-0.469}\, e^{0.239\beta}.$$

The probabilities of detecting a difference between two mortality coefficients, given that there is a difference (this is referred to as the power of the test), were calculated for various sample sizes and listed in Table 7. The power increases as the difference of mortality coefficients increases, and it is equal to the level of

TABLE 7.—Probability of detecting a difference between two mortality coefficients, given one of the mortality coefficients (β_1), the true difference ($D = \beta_2 - \beta_1$), and the number of positive tows (n). Because of symmetry about $D = 0$, partial figures are listed.

	True difference (D)							
n	−2.0	−1.5	−1.0	−0.5	0.5	1.0	1.5	2.0
$\beta_1 = 1.0$								
10					0.62	0.96	1.00	1.00
20					0.86	1.00	1.00	1.00
30					0.96	1.00	1.00	1.00
40					1.00	1.00	1.00	1.00
$\beta_1 = 1.5$								
10				0.50	0.50	0.97	1.00	
20				0.79	0.75	1.00	1.00	
30				0.93	0.90	1.00	1.00	
40				0.98	0.96	1.00	1.00	
50				1.00	0.99	1.00	1.00	
60				1.00	1.00	1.00	1.00	
$\beta_1 = 2.0$								
10			0.96	0.40	0.43	0.92		
20			1.00	0.70	0.70	1.00		
30			1.00	0.86	0.86	1.00		
40			1.00	0.93	0.92	1.00		
50			1.00	0.98	0.96	1.00		
60			1.00	1.00	1.00	1.00		
$\beta_1 = 2.5$								
10		1.00	0.91	0.34	0.48			
20		1.00	0.99	0.59	0.58			
30		1.00	1.00	0.76	0.75			
40		1.00	1.00	0.86	0.86			
50		1.00	1.00	0.93	0.91			
60		1.00	1.00	0.96	0.95			
70		1.00	1.00	1.00	1.00			
$\beta_1 = 3.0$								
10	1.00	0.99	0.82	0.27				
20	1.00	1.00	0.98	0.50				
30	1.00	1.00	1.00	0.66				
40	1.00	1.00	1.00	0.78				
50	1.00	1.00	1.00	0.86				
60	1.00	1.00	1.00	0.91				
70	1.00	1.00	1.00	0.95				
80	1.00	1.00	1.00	0.97				
90	1.00	1.00	1.00	1.00				

significance ($\alpha = 0.05$) when the difference is zero. The power is symmetrical about $D = 0$; thus, only partial figures were given in Table 7.

For example, if the true difference was 0.5 and one of the mortality coefficients was 2.0, with a probability of 0.86, a sample size of 30 positive tows from each of two populations will detect a significant difference in their mortality coefficients. The probability would be only 0.76 if one of the mortality coefficients was 2.5. In general, to achieve the same probability of detecting a given difference between mortality coefficients, a larger sample size is required for a larger β. To detect a significant difference with a probability of 0.96, when the true difference is 0.5 and one of the mortality coefficients is 1.0, 30 positive tows are required from each population. If $\beta = 2.5$, however, 60 positive tows are required to detect the same difference with a probability of 0.95. If the difference is greater than 1, at most 20 positive tows from each population would be sufficient.

The two methods serve different purposes. The *cv* method provides a 95% confidence interval for the difference. The Power Method assigns a probability to the detection of a difference, but provides no information on the magnitude of the difference.

Estimates of β with Various Growth Rates

Mortality is defined as the decline of production with larval age. Thus an overestimate of larval age, predicted from an underestimate of growth rate, will underestimate mortality rate. Similarly, an overestimate of growth rate will result in an overestimate of mortality rate.

The mortality coefficient (β) was fixed at 1.5. Data from February, region 7, temperature 15°C, were used to construct five populations, corresponding to five combinations of growth coefficients for yolk-sac and feeding larvae (Table 8). Each population was surveyed 50 times with a sample size of 50 plankton tows. The estimated mortality coefficient (b) was calculated by assuming standard growth coefficients for February, region 7, temperature 15°C (Table 8). When the population growth coefficients (α_m) were underestimated by the standard coefficients, the estimated mortality coefficient (b) was less than $\beta = 1.5$; conversely when growth was overestimated, the mortality coefficient was also overestimated.

Because the yolk-sac stage is short, relative to the feeding stage, we can reasonably assume that the growth coefficient for feeding larvae (α_m) has the largest effect on the estimated mortality coefficient (b). When the estimated mortality coefficient is plotted against α_m (Fig. 9), it is apparent that the bias in estimating mortality rate, caused by errors in the assumed growth rate, is asymmetrical: greater when actual growth is slower than assumed growth and smaller when actual growth is faster than assumed. When the actual growth was half the assumed rate, the mortality coefficient was overestimated by 80%; when the actual growth was double the assumed rate, the mortality coefficient was underestimated by only 16% (Table 8).

The coefficient, α_m, determines the instantaneous growth rate (IGR) at age t as the IGR = $\alpha_m \ln(L_\infty/L_0) \exp[-\alpha_m(t - t_0)]$ where L_∞ is the maximum fish length, and L_0 is the minimum fish length for $t > 6.28$ days (Fig. 6). Large value of α_m implies that the IGR is large for the small value of age t, and the IGR decreases rapidly as the fish ages. Because both the IGR and the instantaneous mortality rate (IMR = β/t) are two different nonlinear functions of age (t), the relationship between these two coefficients (α_m and β) is also nonlinear and thus the bias is asymmetric.

TABLE 8.—Five sets of coefficients for two-step Gompertz growth curves (Fig. 6) used to simulate five populations. Also listed are the standard coefficients used in the analysis of survey data for region 7 in February with a temperature of 15°C. The estimated mortality coefficient (b) is listed as average of 50 computer runs. The true mortality coefficient (β) was 1.5.

a_T	b_T	α_T	a_m	b_m	α_m	b
0.11	0.06	0.27	44.96	0.83	0.023	2.70
0.11	0.24	4.05	11.24	0.83	0.104	1.26
0.22	0.12	1.33	22.48	0.42	0.046	1.41
0.11	0.09	0.42	33.72	0.83	0.031	1.90
0.22	0.12	1.33	16.86	0.83	0.066	1.31
Standard coefficients:						
0.11	0.12	0.67	22.48	0.83	0.048	

DISCUSSION AND CONCLUSIONS

The simulation model and its methodology have general applicability to larval fish of many species, although these results apply directly to estimates of northern anchovy larval mortality rates derived from CalCOFI surveys. Results may differ because of differences in the param-

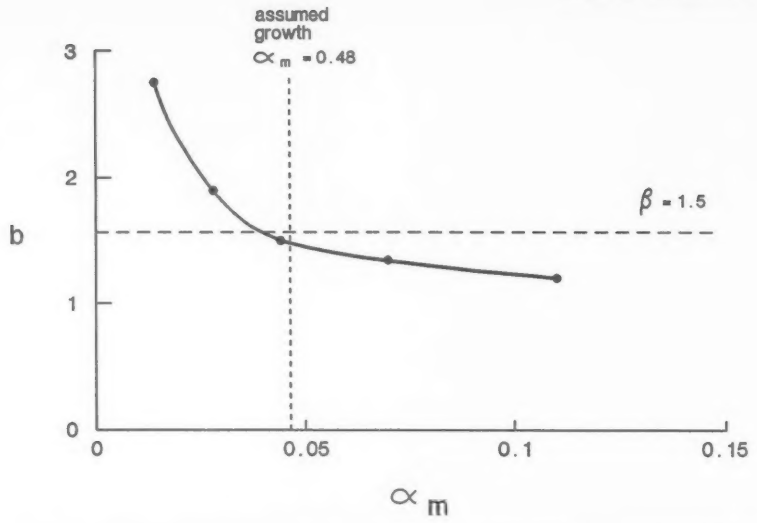


FIGURE 9.—The estimated mortality coefficient (b) is biased by errors in the assumed growth coefficient for feeding larvae, $\alpha_m = 0.48$. The true mortality coefficient (β) was 1.5.

eter values and their variances. Nevertheless, most ichthyoplankton sampling problems are sufficiently similar so that the results derived for anchovy provide a general idea of the sample size required for adequate precision of larval mortality estimates. (When using the regressions derived in this study to estimate sample size, parameter values should be within the range used in the simulation [$1.0 \leq \beta \leq 3.0$, $0.5 \leq D \leq 2.0$]. Values outside these ranges could lead to unreliable estimates of sample size.) The results also provide an assessment of the effect of biased growth rates on estimates of larval mortality rate, which has general applicability to many species.

Caveats

Application to Site-Intensive Studies

Small-scale site-intensive studies may be conducted to study underlying mechanisms of larval mortality rate by measuring larval condition, growth, starvation rates, and mortality rate in small segments of the habitat. Such studies have greater problems with bias and precision than the CalCOFI surveys where the entire spawning habitat is sampled. As noted above, an important potential bias is the transport of larvae in or out of the study area. Taggart and Leggett (1987) noted that failure to account for advective losses of larvae from a small bay resulted in a significant overestimate of mortality.

Another problem arises from the choice of study areas. Many specimens must be collected over a short period to assess growth, starvation, and other condition factors. If sites are selected that contain larval densities that are high, relative to the average density for the entire habitat, and patchy, the effect will be to increase the variance, because the variance is often positively correlated with the density of larvae (Smith and Richardson 1977), and thereby reduce the power to detect differences in mortality rate between sites. The simulations were based on large regions of anchovy habitat and therefore underestimate sample size required to detect mortality rate differences between small areas of high larval abundance.

Application to Other Species

A key difference between larval anchovy and most other species of larval fishes is that anchovy are very abundant. The simulation results indicate that surprisingly few positive tows are needed to detect relatively small differences in mortality rates. In the regions considered in the simulation, 50–60% of the tows were positive, and the number of larvae caught per tow averaged 125, with 88% < 10 mm in length. For a less abundant species, the proportion of positive tows and the average number caught per tow would be much lower, and many more tows

would be required to attain the same level of precision.

Application to CalCOFI Surveys

Three key assumptions underlie the use of the CalCOFI time series of larval mortality estimates for hypothesis testing: 1) a stable age distribution prevails (i.e., abundance of several cohorts of larvae at one moment in time is representative of one cohort as it ages through time), 2) variations in observed mortality rate represent true natural variations and not sampling error, and 3) use of the same larval growth parameters for all years does not bias the estimates of mortality rate.

The first assumption was not addressed in this study. It implies negligible immigration and emigration of larvae and continuous production of spawn. The CalCOFI surveys are designed to encompass the anchovy spawning habitat and thus minimize inaccuracies caused by transport of larvae in and out of the survey area. For a species with a broad temporal spawning curve and with repeated spawning by individuals (9–16% of the females spawn each night; table 7, Fiedler et al. 1986), unbiased estimates of mortality rate may be obtained by pooling plankton tows conducted throughout the spawning season (table 6, Hewitt and Methot 1982). With smaller surveys and shorter time periods, the assumption of a stable age distribution may not be suitable, and estimates of mortality rates may be biased.

With regard to the second assumption, our simulations indicate that the time series of daily mortality rate of anchovy larvae represents predominantly real differences owing to biological variation rather than random variation. Recent CalCOFI ichthyoplankton surveys (Table 9) yielded between 36 and 236 positive tows per spawning season. The simulation model indicates that sample sizes >80 are sufficient to detect a difference of 0.5 or more in the mortality coefficient (β) between years (Table 7). When all possible pairs for the eight surveys (1980–87) are compared, 12 of the 28 comparisons had a difference >0.5 (Table 9). Results of our simulation imply that the precision of past surveys was adequate, and the interannual variation in mortality rate (β ranged from 1.22 in 1980 to 2.14 in 1986) is real.

Because larval mortality rate is age-dependent (IMR = β/t) with high mortality occurring during the onset of feeding and decreasing thereafter, variations in daily mortality rates can be typified by "large differences concentrated in a short period of time" and thus be easily detectable (Gulland 1971). The critical issue in comparing mortality rates does not appear to be one of precision but rather one of obtaining a representative sample.

With regard to the third assumption, the simulation also indicated that the risk of introducing a large bias in estimates of mortality rates by using a single family of standard growth curves is relatively low. A large bias would be expected only when the standard growth curves overestimated the actual growth by a factor of two or more. It is unknown how frequently the standard growth curve generates this large bias, for lack of data on variability of larval growth rates from year to year in the field.

TABLE 9.—Number of tows positive for anchovy larvae (n) and mortality coefficients (β) for CalCOFI ichthyoplankton surveys conducted during January through April 1980–87.

Year	n	β
1980	197	1.22
1981	236	1.53
1982	69	1.81
1983	65	2.05
1984	176	1.47
1985	37	2.03
1986	83	2.14
1987	36	1.98

CONCLUSIONS

These simulations validate the use of CalCOFI survey information to test hypotheses regarding larval survival and recruitment (Butler 1987, Peterman et al. 1988). The sample size required for adequate precision of estimates of mortality rates is modest relative to the one required for adequate representation of the spawning season and habitat of a major marine stock such as the northern anchovy. As stated, the critical issue in comparing mortality rates does not appear to be precision of the estimates but rather how well the sample represents the population.

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APPENDIX

Assignment of Larval Ages Using the Pareto Function

The standing stock (SS) of larvae, between the ages of t_h and 20 days, is the integral of the production curve (Fig. 5) over these ages:

$$SS = \int_{t_h}^{20} P_t\,dt = \int_{t_h}^{20} P_h(t/t_h)^{-\beta}dt$$

$$= [1 - (20/t_h)^{-(\beta-1)}]\frac{t_h P_h}{(\beta - 1)} \qquad \text{for } \beta <> 1,$$

$$= [\ln(20) - \ln(t_h)]t_h P_h \qquad \text{for } \beta = 1.$$

Similarly the number of larvae younger than age t is

$$SS_t = [1 - (t/t_h)^{-(\beta-1)}]\frac{t_h P_h}{(\beta - 1)} \qquad \text{for } \beta <> 1,$$

$$= [\ln(t) - \ln(t_n)]\, t_h P_h \qquad \text{for } \beta = 1.$$

The proportion of larvae that are younger than age t is

$$r(t) = SS_t/SS = \frac{1 - (t/t_h)^{-(\beta-1)}}{1 - (20/t_h)^{-(\beta-1)}} \qquad \text{for } \beta <> 1,$$

$$= \frac{\ln(t/t_n)}{\ln(20/t_h)} \qquad \text{for } \beta = 1,$$

where $0 < r(t) < 1$.

By rearranging terms, t can be expressed as

$$t = t_h[1 - r(t)(1 - (20/t_h)^{-(b-1)}]^{-1/(b-1)} \qquad \text{for } b <> 1,$$

$$= t_h(20/t_h)^{r(t)} \qquad \text{for } b = 1,$$

where b is a normal random variable with mean = β and standard error = 0.2 β (0.2 is an arbitrarily chosen value for the coefficient of variation (b) and $r(t)$ is a uniform random variable between 0 and 1).

Sample Allocation

The allocation of tows to each region and month was based on the 1984 sampling pattern (Table 2, Fig. 2). For a total of N tows, the number of positive tows allocated to month i and region j was computed as

$$n(i,j) = N * p(i) * q(j|i) * r(j|i)$$

where $p(i)$ is the proportion of tows for month i and $\Sigma p(i) = 1$
$q(j|i)$ is the proportion of tows made in region j during month i and $\Sigma q(j|i) = 1$
$r(j|i)$ is the proportion of positive tows for region j during month i and $0 <= r(j|i) <= 1$.

A uniform random number generator was used to assign each tow to a month and region, to determine whether the tow was positive or not, and thus to produce $n(i,j)$.

Assignment of the Time of Tow

Table 3 lists parameters for Gamma distributions fitted to the actual time between positive tows minus the minimum time between any two positive tows (i.e., plankton tows which caught at least one anchovy larva) in each region because the Gamma distribution takes all values to be greater than zero. Each distribution is shifted to the right by the constant listed (the minimum time between any two positive tows). Actual times greater than 150 hours were assumed to be periods of transit to and from port and were thus excluded when fitting the distributions.

The time of the first tow of a simulated survey was chosen randomly and incremented by time intervals selected from the distributions described in Table 3. If the selected time interval was greater than 4 hours, tows with zero catch were inserted. The number of zero tows inserted was the time interval between two positive stations divided by the average travel time between stations (2 hours).

Catchability, Growth, and Mortality of Larval Fishes

Wallace W. Morse

ABSTRACT: The catchability of fish larvae with a 61 cm bongo net was determined from analysis of day, night, and twilight samples from 8,312 stations made off the northeast United States during 1977–84. Night catches exceeded day catches by 62% and twilight exceeded day catches by 44%. Catchability by year and month revealed some variations; however, night catches still dominated. The daily cycle in catchability of all larvae showed that the maximum catch occurred at approximately 0200, and was about 2.5 times the minimum catches at 1700. Changes in catchability with water column depth reflected changes in species composition of the catches.

Analysis of 36 taxa revealed 11 significant differences in day:night, day:twilight, and night:twilight catch ratios. Length-dependent catchability and correction factors were determined for 26 species. Corrected length frequencies were used to calculate length-dependent mortalities which are shown to be positively correlated with water temperature. Larval growth rates were also found to be temperature dependent and, by incorporating a length-weight coefficient, larval length was converted to age. Age-frequencies were used to calculate daily larval mortality and, for most species, the ratio of mortality rate to growth rate was approximately 0.8. Those species with ratios at or over 1.0, i.e., bluefish, *Pomatomus saltatrix*; *Sebastes* spp.; Atlantic mackerel, *Scomber scombrus;* cunner, *Tautogolabrus adspersus*; and, to some extent, haddock, *Melanogrammus aeglefinus*, probably exhibit significant net avoidance.

Surveys of ichthyoplankton in the marine environment have been an integral part of fisheries science for nearly a century. Today large marine ecosystems are routinely monitored for both physical and biological parameters to study multispecies interactions during the early life history of fishes (Sherman 1986). One of the major goals of large marine ecosystem surveys is to monitor the inter- and intra-annual changes in larval fish abundance and mortality and their relationship to recruitment of fishable biomass. Demonstrating the relationship between larval abundance and recruitment has remained elusive owing, in part, to the complexities of the interactions of the physical and biological factors that affect survival of fish during the first year of life. However, a number of theories have been proposed that attempt to link larval fish survival and, by inference, recruitment with their food supply. These include the "critical period" theory (Hjort 1914; May 1974), the "match-mismatch" theory (Cushing 1975), and the mixed layer stability hypothesis (Lasker 1981).

A requisite condition for the testing of these and other theories using broadscale ichthyoplankton surveys is what Zweifel and Smith (1981) call an "effective sampler size". This involves accounting for the "effect of environmental and behavioral factors on the content of the samples or collections". The objective of accounting for these factors is to standardize the sampling gear by applying correction factors in order to minimize sampling variability and to make samples comparable (Smith and Richardson 1977). A key consideration and a possible serious source of bias in larval fish collections is net avoidance (Clutter and Anraku 1968). Fish larvae can avoid capture by swimming out of the path of an approaching net or by migrating below the maximum depth sampled by the net. If detection of an approaching net by larvae is visual, changes in light intensity or net coloration will alter catchability. The magnitude of visually cued avoidance is indicated by the variation in day versus night catches.

Differences in day versus night catches for numerous species have been reported for the past 60 years (e.g., Johansen 1925; Russell 1926; Ahlstrom 1954; Bridger 1956; Miller et al. 1963; Lenarz 1973). In most cases night catches exceed day catches. But there is evidence that gear configuration and towing speed affect the ratio of day-to-night catches (Bridger 1956; Clutter and Anraku 1968). For example, Miller et al. (1963) attributed the lack of difference in day-to-night catches of haddock, *Melanogrammus aeglefinus*, to the high speed (4 m/s) gear they used.

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Accounting for the various sources of sampling bias and for standardizing larval catches facilitates the calculation of the critical population parameters of abundance and mortality. These parameters are the basis for testing the possible effects of biotic and abiotic variables upon larval fish survival and recruitment and are often used to support or reject a particular hypothesis. The general effect of net avoidance is an increase in estimates of mortality (Clutter and Anraku 1968), which in turn can lead to unrealistic conclusions.

The interrelationship of mortality and growth parameters has been firmly established for fishes in the marine ecosystem (Beverton and Holt 1957; Ursin 1967; Ware 1975; Shepherd and Cushing 1980; Peterson and Wroblewski 1984; Houde 1987; and others). The underlying assumptions for this relationship are that mortality is the result of predation and that predation rates decrease as prey size increases. This simplistic model was described as the "cube root rule" (Ursin 1967) where mortality is equal to the cube root of the weight. Peterson and Wrobleski (1984) expanded this relationship to include growth efficiency and metabolism and estimated the annual mortality rate (M) for larval and adult fishes weighing between 10^{-5} and 10^{3} g as $M = (1.92 * \text{year}^{-1}) \text{ weight}^{-25}$. Pauly (1980) noted the rather weak relationship between fish size and mortality ($r^2 = 0.38$) and found that the inclusion of environmental temperature significantly improved the fit ($r^2 = 0.71$) of mortality to maximum length and growth rate for 175 fish stocks. The objectives of this study are to determine the changes in larval fish catches during day, night, and twilight hours and provide correction factors to standardize catches for net avoidance. These corrections can significantly change the abundance and mortality estimates of those species that show a difference in day, night, or twilight catches. Length-dependent larval mortality is estimated from avoidance-corrected abundances for 26 fish taxa and is related to water temperatures. The relationships of larval growth, mortality, and water temperature are explored to determine if net avoidance is, in fact, a serious problem as it relates to estimtes of larval mortality.

METHODS

Continental shelf and slope waters off the northeast United States have been sampled six to eight times each year since 1977 to provide information on the distribution and abundance of fish eggs and larvae as well as to provide fisheries independent estimates of spawning biomass. A total of 8,312 stations were occupied from 1977 through 1984 between Cape Hatteras, NC, and Nova Scotia (Fig. 1). At each station a 61 cm bongo net frame, fitted with 505 μ and 333 μ mesh nets and flowmeters, was lowered at 50 m/min to within 5 m of the bottom or to 200 m maximum and retrieved at 20 m/min. Ship speed was adjusted to maintain a wire angle of 45 degrees; the 505 μ mesh net was used for ichthyoplankton analysis; and samples were preserved in 5% formalin. All fish larvae were identified to the lowest taxon possible, enumerated, and measured to the nearest 0.1 mm standard or notochord length. If more than 50 specimens of a particular taxon were captured in a tow, then 50 randomly selected larvae were measured. Water temperature profiles were taken at each station. A detailed account of all shipboard and laboratory methods, and sampling locations is provided in Sibunka and Silverman (1984).

Larval catches were standardized (S) to the number under 10 m^2 of sea surface by the equation:

$$S = 10 * N * D * A^{-1} * M^{-1} \qquad (1)$$

where N is the number of larvae in the sample, D is the maximum depth of the tow in meters, A is the area of the mouth of the net, and M is the distance the net was towed in meters determined from the calibrated flowmeter (Smith and Richardson 1977). All analyses followed standardizing of catches to the number of larvae under 10 or 100 m^2 and rounding of lengths to the nearest mm.

Each station was assigned to day, night, or twilight hours according to the recorded time at the beginning of the tow. Twilight was designated as one hour before and after both sunrise and sunset while day or night was assigned between the two twilight intervals.

Catches of all larvae were analyzed by hour of the day to determine if a daily cycle in catchability could be detected. The assumption in this analysis is that the daily cycle of incident light is the controlling factor for visual detection of the net. The seasonal and latitudinal changes in the duration of daylight hours (e.g., 8.6 hours in winter to 15.4 hours in summer) made it necessary, in order to maintain equivalent light regimes across seasons and areas in the analysis, to partition the day into 24 intervals of 10 for

daylight, 10 for nighttime, and 2 for each of the twilight times. The number of hours (H) between sunrise and sunset for each station was calculated using latitude and Julian day (Iqbol 1983), as follows

$$H = -7.6393 * \arcsin[\sin(L) * \sin(C)/(\cos(L) * \cos(C))]$$

where $L = 0.0172(\text{latitude})$.

$$C = 0.3964 - 22.9133 * \cos(Z) + 4.1580 * \sin(Z) - 0.3964 * \cos(2Z) + 0.5197 * \sin(2Z) - 0.1545 * \cos(3Z) + 0.0848 * \sin(3Z), \text{ and}$$

$$Z = 0.0172\ (\text{Julian day} - 1).$$

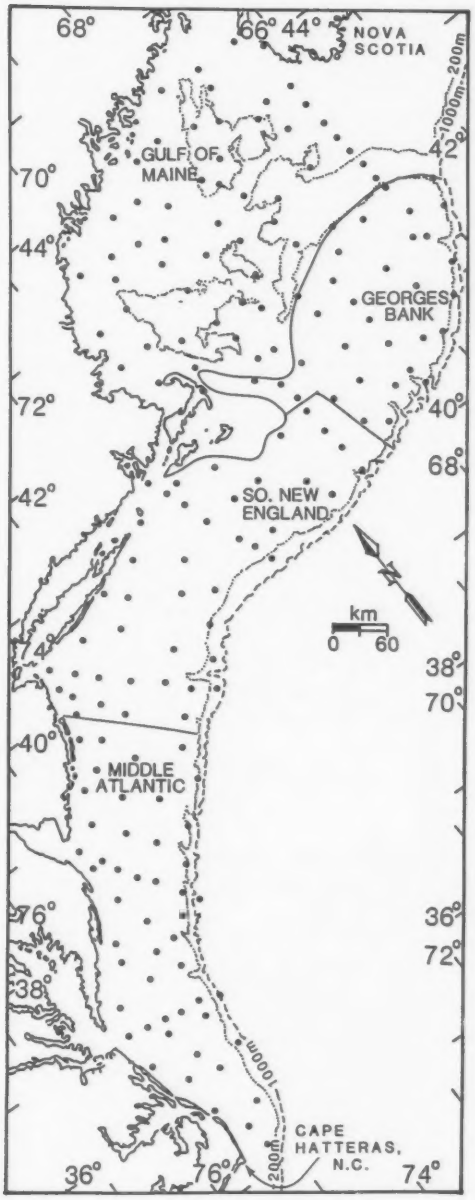


FIGURE 1.—Map of area surveyed, station locations and subareas off the northeast United States.

Twilight hours remained one hour before and after sunrise and sunset and were partitioned into hour intervals 5–6 and 17–18, respectively, and accounted for 4 of the 24 h day. The remaining daylight hours ($H - 2$), where H is time from sunrise to sunset, were partitioned into 10 equal intervals (i.e., hours 7–16). Nighttime hours ($24 - (H + 2)$) were also partitioned into 10 intervals corresponding to hours 0–4 and 19–23. The time interval for a daylight "hour" ranged from about 52 minutes in winter to 92 minutes in summer. Each station was assigned an "hour" interval and analysis was performed during this interval.

The occurrence of tows that did not contain larvae or that did not contain the particular taxon of interest presented a special problem in day-versus night-catch analysis. The absence of larvae might have occurred because there were no larvae within the path of the net or because of net avoidance by the larvae. This being the case, all stations in cruises that contained at least one occurrence of the taxon being investigated, except where noted, were included in calculations of mean catch per 10 m^2. The result of including these zero tows was a reduction in the mean catch, but a stability in the catch ratios. In addition, the survey area was divided into four subareas: Middle Atlantic Bight (MAB), Southern New England (SNE), Georges Bank (GB), and Gulf of Maine (GOM) (Fig. 1). The subareas were used to stratify the entire survey area during analysis for those taxa that spawn in a limited area. For example, if no larvae of a particular species were caught in GOM subarea then all GOM stations were ignored for the analysis of that species. The calculation of the mean catch and its variance using zero tows followed the methods of Pennington (1983) for the Delta distribution of catch frequencies. Ratios of all larvae for day, night, and twilight were based on mean catch per 10 m^2, and ratios for millimeter length increments were based on mean catch per

100 m^2. Other statistics were calculated according to Zar (1984).

The analysis to derive correction factors for day, night, and twilight catchability and to derive estimates of larval mortality for 26 species involved three steps. The larval length-interval used was calculated from the modal length, which was always greater than the minimum length captured, to the maximum length that was captured in all three light regimes. I assumed that the modal length was the minimum length fully retained by the 505 μ mesh net. If extrusion of larvae at modal lengths or greater is significant, length-dependent mortalities will be underestimated and will have no effect on catch ratios. The exponential decay regression model was fitted to the larval length (X_i) and catch per 100 m^2 (Y_i) as

$$Y_i = \alpha \exp(-\beta X_i) + \epsilon_i \quad (2)$$

for each species by day, night, and twilight catches. The expected catches from these regressions were then used to estimate the ratios of catch by length for night:day and twilight:day. The predictive nonlinear second-order polynomial regression model:

$$R_i = \alpha + \beta_i X_i + \beta_1 X_i^2 + \epsilon_i \quad (3)$$

was fitted to the ratios by length. (The predicted ratio (R_i) of night:twilight catches for any length (X_i) is, of course, the ratio of night:day at X_i divided by the twilight:day ratio at X_i.) The catches at each length per 100 m^2 were then corrected using the predicted ratios that maximized the catches. The exponential decay model was again fitted to the corrected catches and the slope of the line was used as an estimate of length-dependent mortality.

RESULTS

All Larvae

The initial analysis examined the catches for all taxa combined for all 8,312 stations, of which 6,530 contained fish larvae. The mean catch per 10 m^2 was calculated for 3,578 day stations, 3,332 night stations, and 1,402 twilight stations (Table 1). A significant difference ($P < 0.05$) was found between night-versus-day and night-versus-twilight catches with the ratios of the mean catches of 1.62:1 and 1.44:1, respectively. The combining of all data raises the question of whether one or more year's data might have been anomalous and produced the significant difference in catches. Each year was analyzed separately and is shown in Table 1. For each year the highest mean catches always occurred at night and in six of the eight years twilight catches exceeded day catches. In four of the eight years a significant difference ($P < 0.05$) was found between night and day catches (1977, 1982–84). The consistent interannual relationships in catches indicate that the combined years' ratios are good indicators of average catchability of all larvae during the 8 yr study.

The analysis of the combined data-set integrates the areal and temporal heterogeneity in the distribution and abundance inherent within the larval fish community. To determine if the

TABLE 1.—The mean catch per tow (#/10 m^2) by day, night, and twilight of fish larvae collected off the northeast United States for years 1977–84 and combined. Numbers in parenthesis are standard error of the mean and sample size. Values of Student *t* test for differences in mean catches.

				t-value		
Year	Day (D)	Night (N)	Twilight (T)	D vs. N	D vs. T	N vs. T
1977	162.868(20.774,591)	260.308(34.274,555)	206.796(46.380,209)	2.4649*	0.9871	0.8536
1978	143.513(22.610,434)	197.502(34.681,401)	121.823(27.723,178)	1.3233	0.5488	1.3698
1979	159.847(19.779,410)	228.784(34.595,178)	170.466(32.641,153)	1.7871	0.2793	1.0248
1980	154.223(20.147,455)	241.296(35.886,397)	187.856(40.815,164)	2.1845	0.8096	0.8661
1981	195.026(27.800,426)	264.761(36.220,412)	178.697(33.435,180)	1.5336	0.3403	1.4562
1982	127.302(18.571,372)	237.059(37.154,366)	126.952(28.913,154)	2.6552*	0.0102	1.8262
1983	134.868(20.838,401)	265.698(47.486,396)	215.808(57.246,172)	2.5379*	1.6468	0.6142
1984	145.628(18.225,489)	287.115(41.634,452)	169.497(32.560,192)	3.1947**	0.6719	1.7468
All	155.379(7.948,3578)	251.673(14.582,3332)	174.533(13.931,1402)	5.9058**	1.2435	3.1837**

* = $P < 0.05$.
** = $P < 0.01$.

ratios of day, night, and twilight catches show seasonal or areal differences, separate ratios of the mean catch per 10 m^2 were calculated for each month for all subareas and by subarea (Table 2). In all months the ratios of night-versus-day catches for all subareas combined were greater than one. Night-to-day ratios ranged from 1.01 in September to 3.23 in January and the mean for all months was 1.82 (SD = 0.56). The extreme values in January and September may be related to the relatively low sample sizes for these two months; however, the higher catches at night relative to both day and twilight catches remained quite consistent regardless of month.

Considerably more variability in the ratios between months is evident when each subarea is analyzed separately, but the general trend of dominance in night catches is still evident within each subarea. The extraordinarily low ratio for twilight-versus-day catches for January in the Gulf of Maine results from a few extremely high twilight catches and relatively low sampling intensity (N = 17).

Catches of all larvae grouped by water column depth are shown in Figure 2. They peak at

TABLE 2.—Ratios of night (N):day (D) and twilight (T):day (D) mean catches of larval fish caught off the northeast United States, 1977–84, by subarea and combined by month. n = number of samples; MAB = Middle Atlantic Bight; SNE = Southern New England; GB = Georges Bank; GOM = Gulf of Maine.

	All			MAB		SNE		GB		GOM	
Month	n	N/D	T/D	N/D	T/D	N/D	T/D	N/D	T/D	N/D	T/D
Jan.	166	3.23	0.37	—	—	—	—	1.47	0.58	1.85	0.07
Feb.	536	1.92	1.15	2.38	1.00	0.81	0.68	1.19	1.25	2.70	4.35
Mar.	906	1.51	1.02	1.33	0.86	1.47	1.39	0.90	0.41	0.47	1.92
Apr.	897	1.45	0.96	2.13	1.75	1.56	1.12	1.15	0.56	0.59	0.45
May	1,112	1.49	1.11	1.10	0.56	1.88	1.64	1.52	1.23	1.28	1.69
June	727	2.43	1.16	2.63	0.79	1.89	1.27	1.01	1.30	3.23	0.99
July	690	2.00	1.06	2.86	1.47	1.20	0.84	7.69	1.75	1.09	0.46
Aug.	850	1.69	1.32	1.25	1.89	2.50	1.19	1.47	1.33	1.35	0.84
Sept.	277	1.01	0.83	1.24	0.79	0.99	—	—	—	—	—
Oct.	1,015	1.75	1.04	0.94	0.42	1.75	1.61	1.85	1.45	2.00	0.56
Nov.	654	1.69	1.85	0.68	0.66	2.01	2.13	1.85	0.43	4.54	7.14
Dec.	482	1.68	1.64	—	—	0.76	1.79	3.23	6.25	4.76	0.91

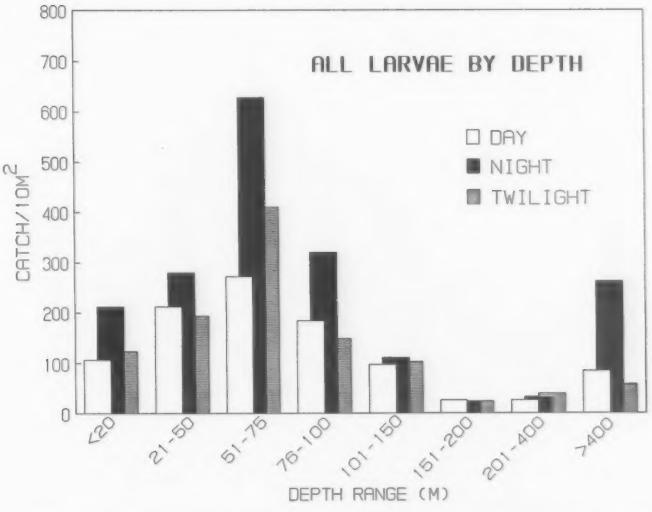


FIGURE 2.—Mean catch of all larvae by bottom depth interval for day, night, and twilight.

depths between 51 and 75 m, decrease to a low at 151–200 m, and then increase again at depths >400 m. The increase in catch per tow at the deep water stations is due to the dominance of two mesopelagic lantern fishes, *Ceratoscopelus maderensis* and *Benthosema glaciale*, which account for 47% of all larvae at these depths. Night catches exceeded day and twilight catches except between 101 and 400 m. At these water column depths the dominant taxa are *Sebastes* spp.; silver hake, *Merluccius bilinearis*; offshore hake, *Merluccius albidus*; Gulf Stream flounder, *Citharichthys arctifrons*; *Urophycis* spp.; Atlantic herring, *Clupea harengus*; and *Ammodytes* spp., all of which comprise 71% of the total catch. The twilight catch at column depths between 101 and 150 m exceeds both the night and day catches and reflects the high twilight catches for Gulf Stream flounder, offshore hake, and to some extent butterfish, *Peprilus triacanthus*.

The daily cycle in mean catch per 10 m^2 for all larvae is shown in Figure 3a. Catches were highest between hour intervals 1 and 6, with maximum catches at hour 2. Minimum catches occurred between intervals 10 and 17 and averaged only 39% of the catch at interval 2. The ratios of the catch at each hour interval, divided by the

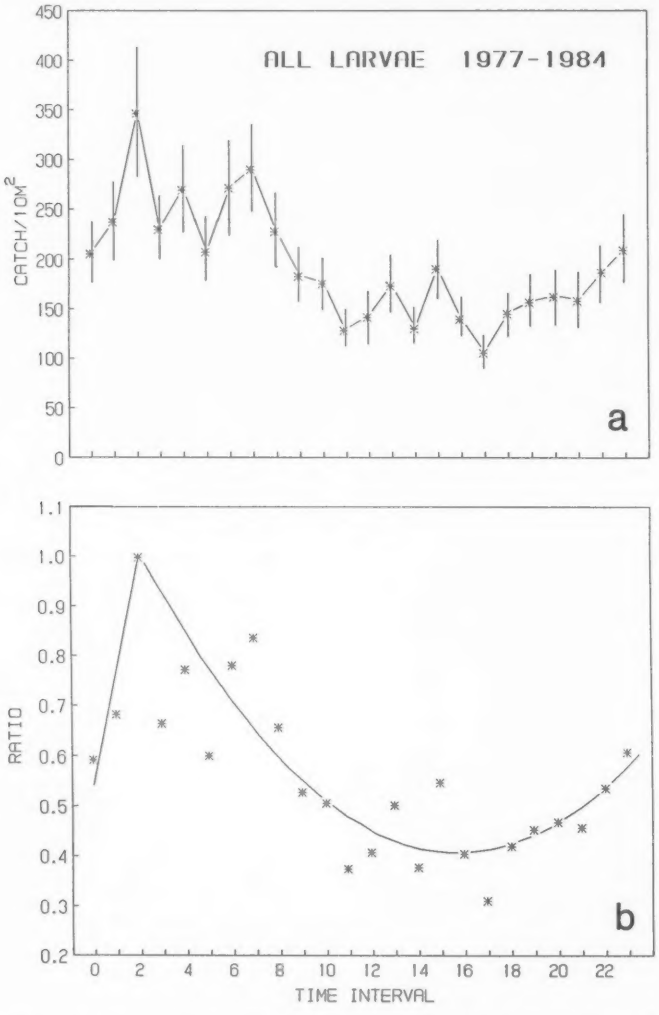


FIGURE 3.—Mean catch per 10 m^2 by time intervals and standard error bars and plot of ratios of catch at time interval 2 with the fitted curves.

catch at hour 2, yield a correction factor to standardize the catch of all larvae for net avoidance. Two linear functions were fit to the ratios for hour intervals 0–2 and intervals 2–23 for the purpose of calculating the correction factor to account for the daily cycle in catches (Fig. 3b).

The equations are

$$C = 0.5575 + 0.2025 * H$$
$$r^2 = 0.91 \quad n = 3 \quad \text{for } H < 3$$

$$C = 1.1992 - 0.1012 * H + 0.00323 * H^2$$
$$r^2 = 0.81 \quad n = 21 \quad \text{for } H > 2$$

where C = the correction factor and H = the hour interval.

Individual Taxa

A total of 36 taxa, representing 17 families, were analyzed for day, night, and twilight catches based upon their abundance within the data set. These taxa represented fewer than 11% of all taxa caught during the 8 yr study but account for over 90% of all larvae captured. They were selected because their abundance is adequate for statistical comparisons of catches. Of the 36 taxa, four were identified to the generic level due to the uncertainty of species identifications, the rest to the specific level. Table 3, a phylogenetic listing (Robins et al. 1980) of the catch data, analyzes the variance (ANOVA) of the delta mean catch per 10 m^2 for each of the 36 taxa by day, night, and twilight and presents Tukey tests of paired means when the ANOVA showed significant differences. The ANOVA showed that the catches of 11 of the 36 taxa have significant differences: day versus night for 9 taxa, day versus twilight for 1 species, and night versus twilight for 7 species. It is interesting to note that the first three taxa listed in Table 3, i.e., the top of the phylogenetic list, contain 25% of all the significant differences found.

In a review of larval swimming needs, Theilacker and Dorsey (1980) showed that jack mackerel, *Trachurus symmetricus*; Pacific mackerel, *Scomber japonicus*; and herring, *Clupea harengus* (two short-bodied and a long-bodied morph) are fast swimmers while sardine, *Sardina pilchardus*; and northern anchovy, *Engraulis mordax* (two long-bodied larvae) are slow swimmers. The implication is, of course, that fast swimming larvae will avoid the approaching net and are most likely to show differences between day and night catches. The larvae of Atlantic menhaden, *Brevoortia tyranus*; Atlantic herring, *C. maderensis*; and *Ammodytes* spp. are long-bodied, while *B. glaciale*; Atlantic mackerel, *Scomber scombrus*; and *Auxis* spp. are short-bodied. At this point no clear relationship seems evident between general morphology and net avoidance; in fact, the results of this study appear counterintuitive.

The occurrences of the 11 significant differences shown in Table 3 are surprising, given the length frequencies of most species considered. The dual effects of larval mortality and net avoidance produce an exponential decline in the abundance of larvae with increasing length. This results in a concentration of larval abundance in the smallest length intervals (usually 3–7 mm), which should be the lengths that are least able to avoid the net. Because of the preponderance of small larvae in the catches, the mean catch per 10 m^2 most reflects the abundance of these small larvae, and thus the statistical significance or insignificance of the differences in catches may not reveal the changes in catchability with increasing larval length. It is interesting to note that 29 of the 36 taxa (81%) show higher night catches than day catches, though statistical significance is met in only 9 taxa.

The changes in catchability with length were investigated by calculating the mean catch per 100 m^2 for each mm length-increment by day, night, and twilight for 26 taxa (Fig. 4). The range of lengths for each species does not show the entire length range captured; rather, they show sequential lengths where positive day, night, and twilight catches were made. For example, *Ammodytes* spp. were captured during day, night, and twilight between lengths 3 and 32 mm but the total length range represented in the 8 yr data set is 1–141 mm. Obviously a mean catch-per-tow of zero cannot be corrected for net avoidance and is therefore not considered in this analysis.

The most common ratios of catches, and the most easily explained in terms of visual net avoidance, are night equals or exceeds day catches, with increasing ratios as larval length increases. The ratios for each length of night:day for expected catches from the regression analysis follow this pattern for 17 of the 26 species analyzed. The magnitude of the difference between night and day varies greatly between species, but the general trend is clearly evident in all 17 species. The only species that shows day catches exceeding night catches at all lengths is

TABLE 3.—Mean larval fish catches per 10 m^2 for day, night, and twilight made off the
significant differences. Numbers in parenthesis

Taxa	Day (D)	Night (N)
Brevoortia tyranus[1] Atlantic menhaden	0.656(0.180,847)	3.434(1.036,861)
Clupea harengus[2] Atlantic herring	3.943(0.941,1314)	10.048(1.846,1589)
Ceratoscopelus maderensis[3]	0.982(0.181,1759)	5.652(0.925,1532)
Benthosema glaciale	1.725(0.305,2201)	2.066(0.329,1928)
Lophius americanus Goosefish	0.621(0.052,2543)	0.488(0.053,1994)
Urophycis spp. hakes	21.505(2.221,2668)	25.563(2.967,2294)
Enchelyopus cimbrius Fourbeard rockling	0.694(0.073,2675)	0.838(0.103,2327)
Gadus morhua Atlantic cod	2.441(0.285,2813)	2.218(0.248,2685)
Melanogrammus aeglefinus[3] Haddock	6.250(1.031,1456)	4.838(1.058,1211)
Pollachius virens[2] Pollock	0.683(0.095,1961)	1.083(0.141,2044)
Merluccius albidus Offshore hake	1.289(0.216,1838)	1.662(0.315,1597)
Merluccius bilinearis Silver hake	13.442(1.408,2514)	15.814(1.794,2239)
Centropristis striata[1] Black seabass	1.151(0.186,1274)	1.841(0.334,955)
Pomatomus saltatrix[1] Bluefish	16.212(2.814,931)	25.967(6.050,585)
Cynoscion regalis[1] Weakfish	0.894(0.230,908)	1.515(0.487,695)
Micropogonias undulatus[1] Atlantic croaker	5.083(2.144,893)	4.806(1.733,812)
Tautogolabrus adspersus Cunner	3.778(0.518,1363)	8.557(1.528,966)
Tautoga onitus[1] Tautog	0.337(0.079,761)	0.688(0.251,498)
Lumpenus lumpretaeformis[3] Snakeblenny	0.500(0.145,700)	0.250(0.070,581)
Ulvaria subbifurcata[3] Radiated shanny	0.462(0.152,633)	0.656(0.185,401)
Pholis gunnelus Rock gunnel	0.405(0.085,1245)	0.564(0.090,1164)
Ammodytes spp. Sand lances	48.001(5.311,2267)	125.737(15.608,2125)
Auxis spp. Mackerels	2.326(0.500,590)	7.549(1.838,397)
Scomber scombrus Atlantic mackerel	18.195(4.133,1284)	35.886(10.866,772)
Peprilus triacanthus Butterfish	5.299(0.507,2566)	6.025(0.716,2019)
Sebastes spp.[3] Redfishes	2.276(0.295,1541)	3.006(0.467,1169)
Myoxocephalus octodecemspinosus Longhorn sculpin	0.249(0.056,707)	0.699(0.132,731)
Citharichthys arctifrons[2] Gulf Stream flounder	16.288(1.882,1970)	19.577(2.511,1620)
Etropus microstomus[1] Smallmouth flounder	5.977(0.755,1658)	7.873(1.125,1339)
Paralichthys dentatus[2] Summer flounder	1.795(0.262,1458)	2.135(0.260,1554)
Paralichthys oblongus[2] Fourspot flounder	8.089(0.689,1691)	7.578(0.785,1324)
Scophthalmus aquosus[2] Windowpane flounder	2.694(0.246,2174)	3.348(0.319,1864)
Hippoglossoides platessoides[3] American plaice	1.580(0.427,989)	1.268(0.276,700)

northeast United States during 1977–85 and analysis of variance (F) and Tukey (q) tests for are standard error of the mean catch and sample size.

Taxa	Twilight (T)	F value	q		
			D:N	D:T	N:T
Brevoortia tyranus[1] Atlantic menhaden	2.072(1.079,340)	3.542*	**	—	—
Clupea harengus[2] Atlantic herring	7.137(2.276,620)	3.898**	**	—	—
Ceratoscopelus maderensis[3]	2.125(0.636,642)	15.928**	**	—	*
Benthosema glaciale	1.781(0.392,838)	0.328			
Lophius americanus Goosefish	0.508(0.073,920)	1.814			
Urophycis spp. hakes	28.091(5.008,991)	1.085			
Enchelyopus cimbrius Fourbeard rockling	0.707(0.126,1008)	0.760			
Gadus morhua Atlantic cod	1.552(0.260,1106)	1.776			
Melanogrammus aeglefinus[3] Haddock	3.967(0.961,550)	0.982			
Pollachius virens[2] Pollock	0.705(0.141,813)	3.361*	*	—	—
Merluccius albidus Offshore hake	3.284(0.842,682)	5.584**		**	*
Merluccius bilinearis Silver hake	12.235(1.940,964)	0.977			
Centropristis striata[1] Black seabass	0.857(0.256,433)	3.020*	—	—	*
Pomatomus saltatrix[1] Bluefish	10.948(3.418,313)	2.467			
Cynoscion regalis[1] Weakfish	0.981(0.313,331)	0.922			
Micropogonias undulatus[1] Atlantic croaker	0.842(0.348,327)	0.838			
Tautogolabrus adspersus Cunner	4.217(1.052,467)	6.633**	**	—	*
Tautoga onitus[1] Tautog	0.527(0.223,244)	1.275			
Lumpenus lumpretaeformis[3] Snakeblenny	0.272(0.147,273)	1.307			
Ulvaria subbifurcata[3] Radiated shanny	0.436(0.224,192)	0.403			
Pholis gunnelus Rock gunnel	0.482(0.119,494)	0.862			
Ammodytes spp. Sand lances	71.144(10.956,896)	13.376**	**	—	**
Auxis spp. Mackerels	2.091(0.891,194)	6.901**	**	—	*
Scomber scombrus Atlantic mackerel	15.607(5.899,410)	2.128			
Peprilus triacanthus Butterfish	5.741(0.918,915)	0.372			
Sebastes spp.[3] Redfishes	1.985(0.350,560)	1.580			
Myoxocephalus octodecemspinosus Longhorn sculpin	0.324(0.122,329)	4.853**	**	—	—
Citharichthys arctifrons[2] Gulf Stream flounder	21.337(4.178,703)	0.943			
Etropus microstomus[1] Smallmouth flounder	3.921(0.947,589)	2.946			
Paralichthys dentatus[2] Summer flounder	1.872(0.402,600)	0.452			
Paralichthys oblongus[2] Fourspot flounder	7.705(1.235,597)	0.125			
Scophthalmus aquosus[2] Windowpane flounder	3.647(0.626,787)	1.928			
Hippoglossoides platessoides[3] American plaice	2.614(1.237,329)	1.093			

TABLE 3.—*Continued.*

Taxa	Day (D)	Night (N)
Glyptocephalus cynoglossus Witch flounder	0.908(0.080,2716)	0.987(0.120,2122)
Limanda ferruginea Yellowtail flounder	5.488(0.510,2110)	8.241(0.963,1492)
Pseudopleuronectes americanus Winter flounder	0.358(0.063,1317)	0.561(0.116,907)

* = $P < 0.05$.
** = $P < 0.01$.
[1]samples from Middle Atlantic Bight and Southern New England subareas.
[2]samples from Middle Atlantic, Southern New England, and Georges Bank subareas.
[3]samples from Southern New England, Georges Bank, and Gulf of Maine subareas.

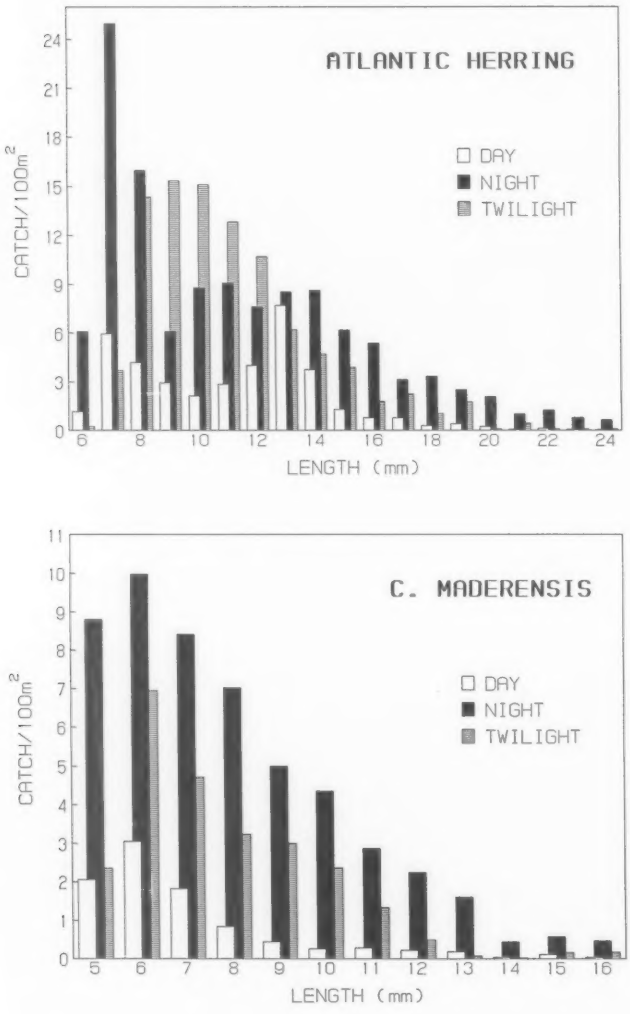
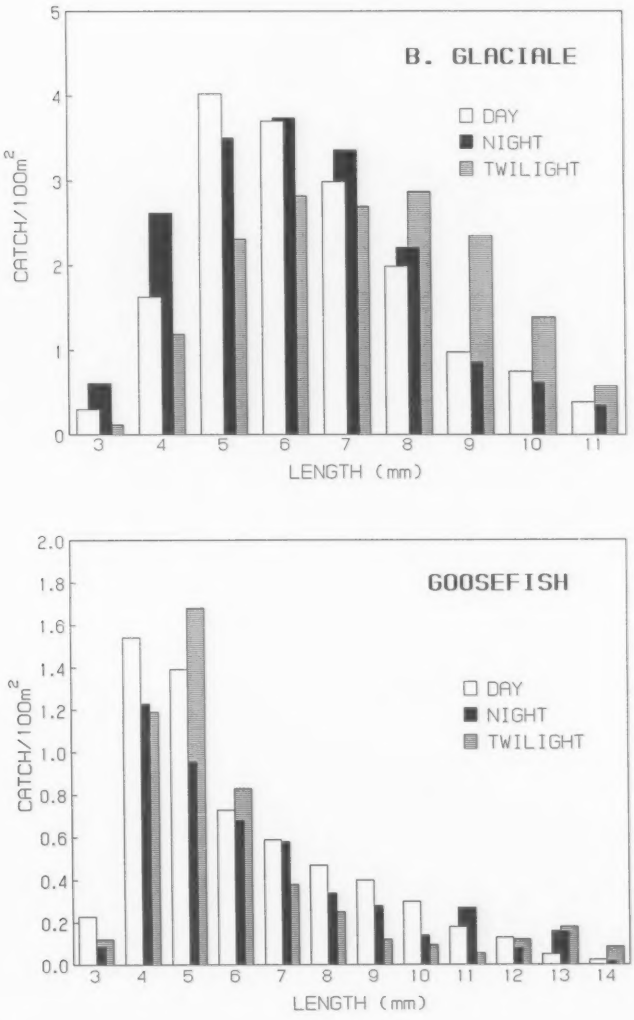
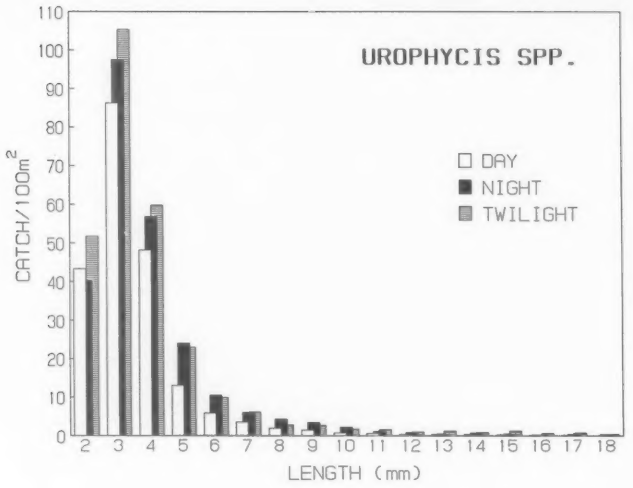


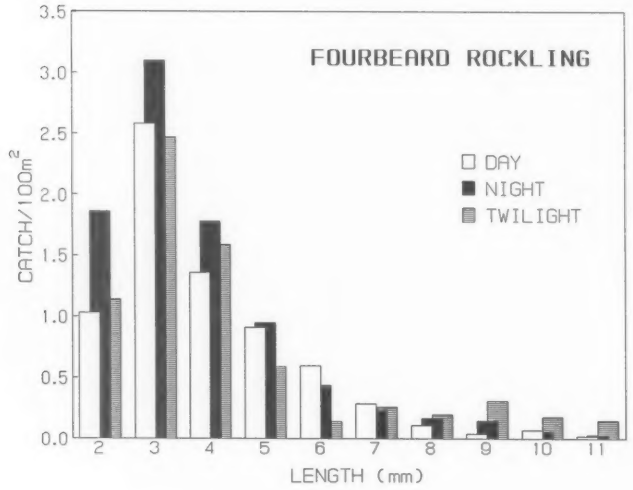
FIGURE 4 a–g.—Plots of mean catch per 100 m^2 by length for day, night, United States,

Taxa	Twilight (T)	F value	q		
			D:N	D:T	N:T
Glyptocephalus cynoglossus Witch flounder	0.702(0.102,974)	1.297			
Limanda ferruginea Yellowtail flounder	5.589(0.972,706)	4.237*	**	—	*
Pseudopleuronectes americanus Winter flounder	0.388(0.127,453)	1.460			



and twilight for 26 taxa of fish larvae collected off the northeast
1977–84.





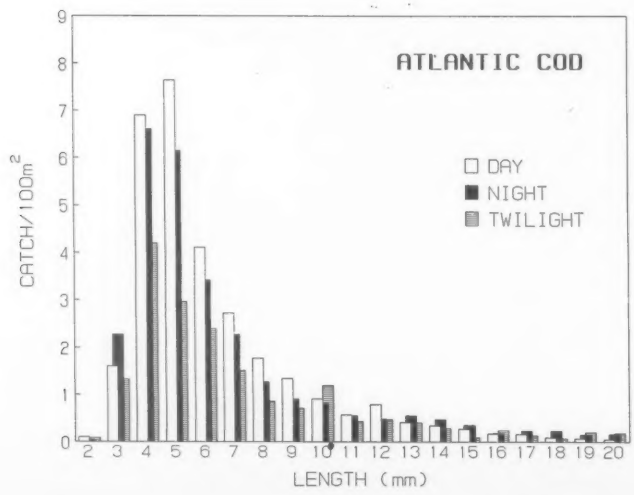
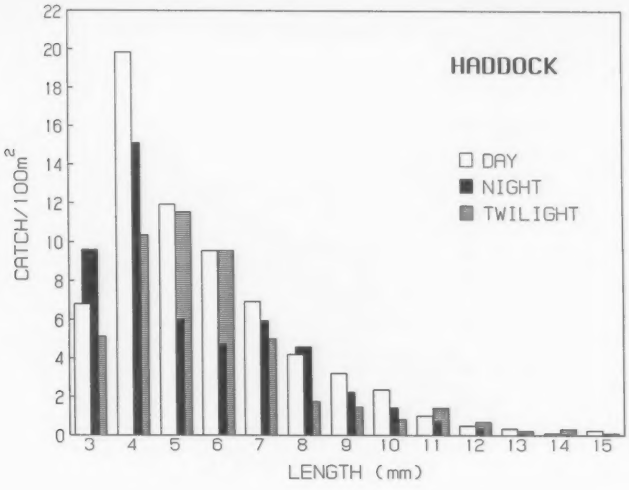
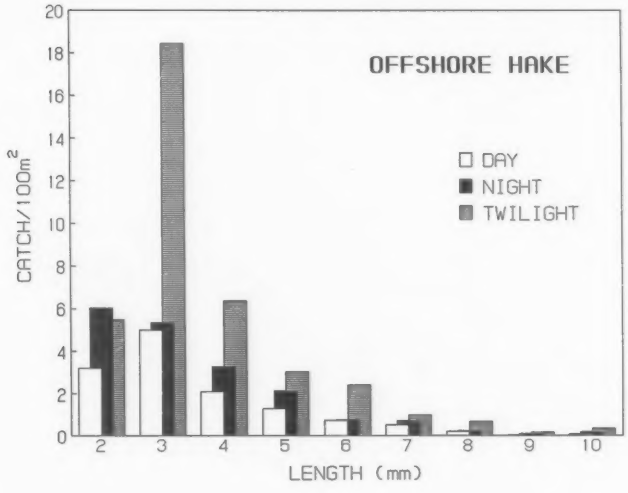
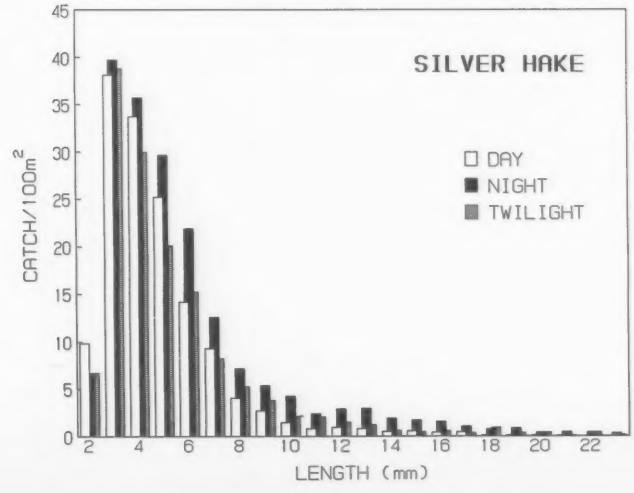
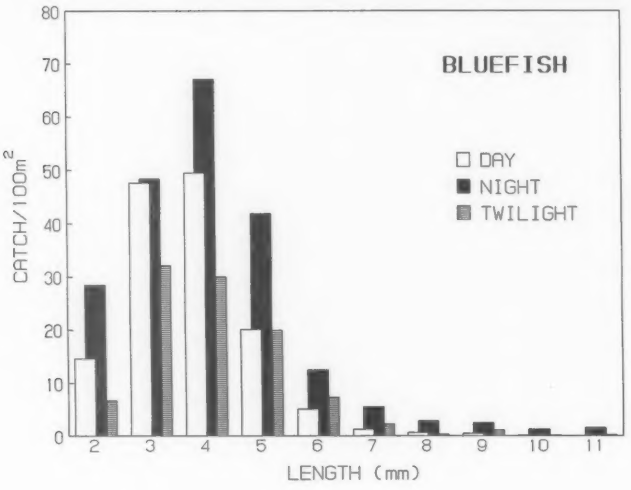


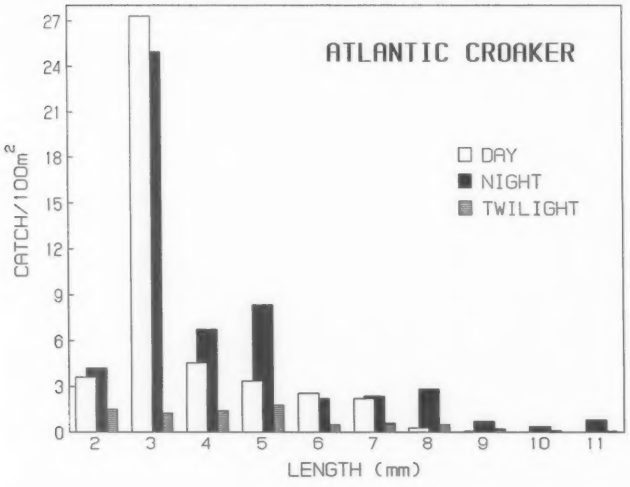
FIGURE 4.—*Continued.*


HADDOCK
DAY
NIGHT
TWILIGHT
CATCH/100m²
LENGTH (mm)


OFFSHORE HAKE
DAY
NIGHT
TWILIGHT
CATCH/100m²
LENGTH (mm)


SILVER HAKE
DAY
NIGHT
TWILIGHT
CATCH/100m²
LENGTH (mm)





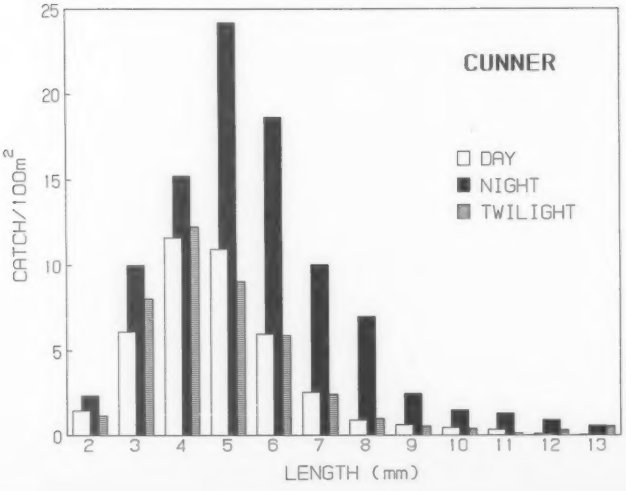
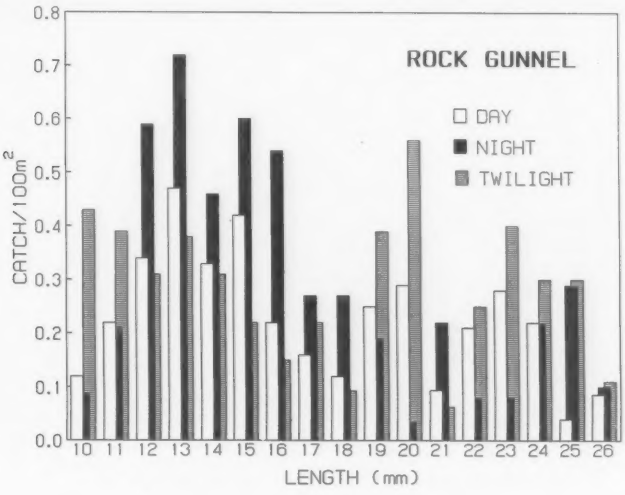
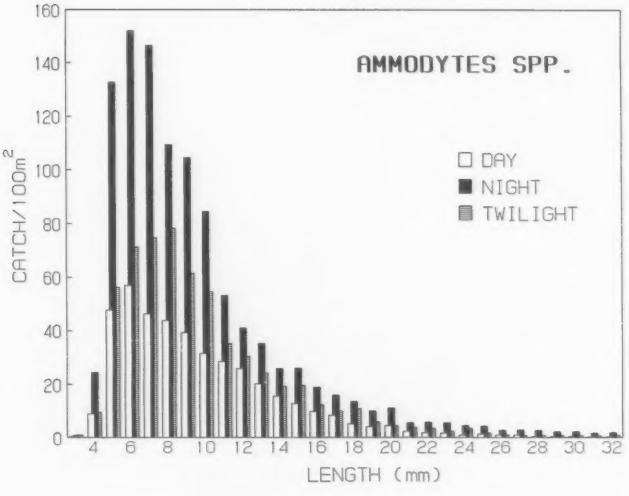
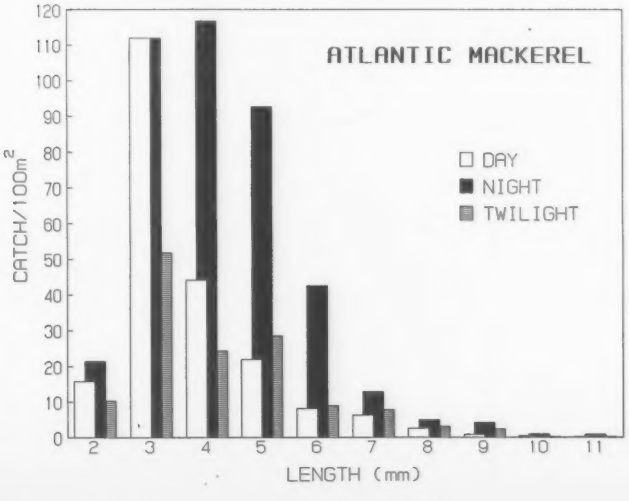
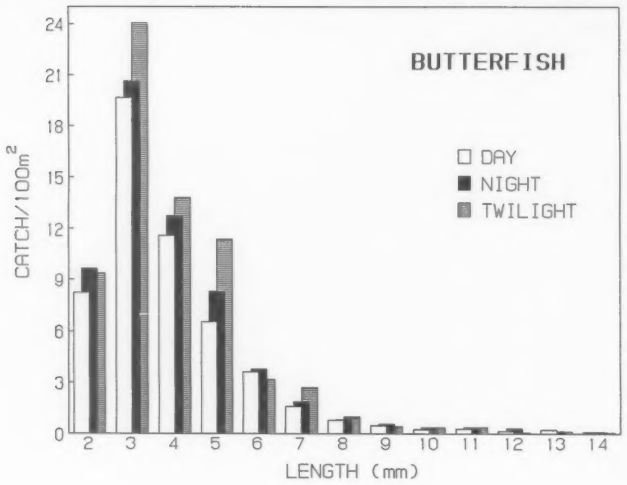


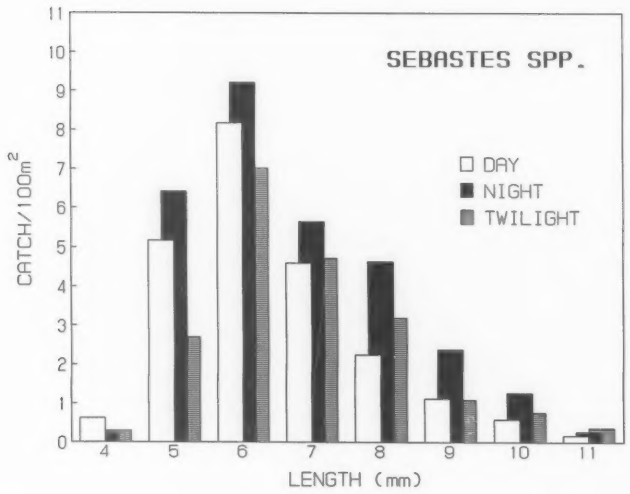
FIGURE 4.—*Continued.*


ROCK GUNNEL
DAY
NIGHT
TWILIGHT
CATCH/100m²
0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8
10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26
LENGTH (mm)


AMMODYTES SPP.
DAY
NIGHT
TWILIGHT
CATCH/100m²
0 20 40 60 80 100 120 140 160
4 6 8 10 12 14 16 18 20 22 24 26 28 30 32
LENGTH (mm)


ATLANTIC MACKEREL
DAY
NIGHT
TWILIGHT
CATCH/100m²
0 10 20 30 40 50 60 70 80 90 100 110 120
2 3 4 5 6 7 8 9 10 11
LENGTH (mm)





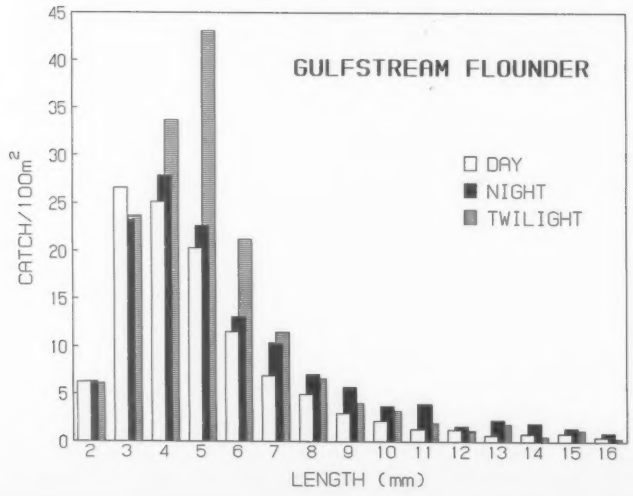
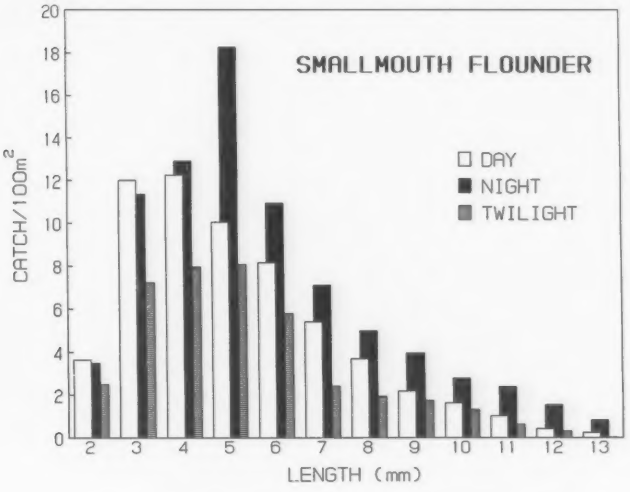
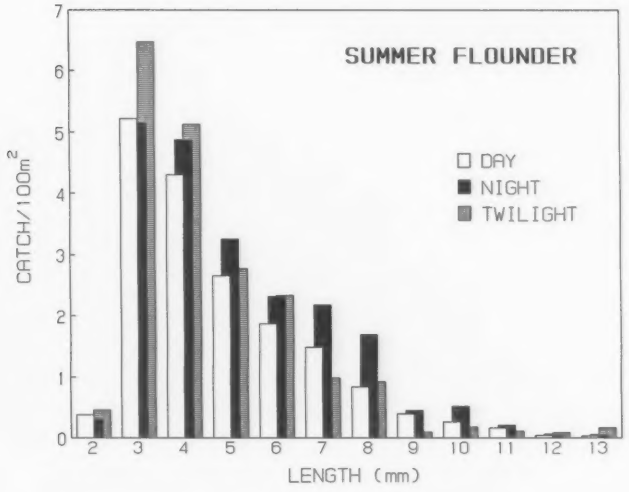
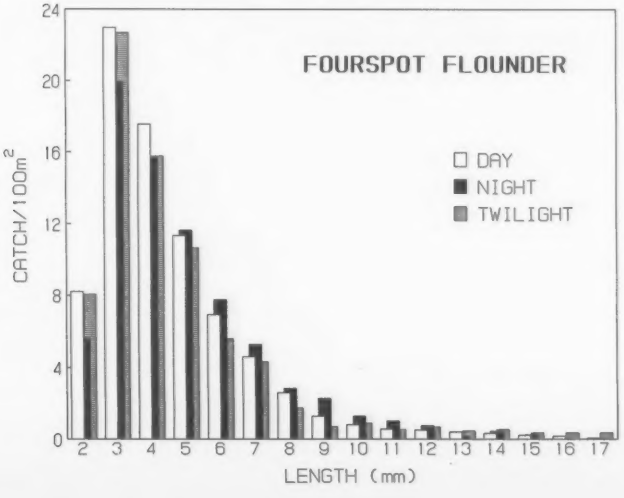


FIGURE 4.—*Continued.*


SMALLMOUTH FLOUNDER
DAY
NIGHT
TWILIGHT
CATCH/100m²
LENGTH (mm)


SUMMER FLOUNDER
DAY
NIGHT
TWILIGHT
CATCH/100m²
LENGTH (mm)


FOURSPOT FLOUNDER
DAY
NIGHT
TWILIGHT
CATCH/100m²
LENGTH (mm)

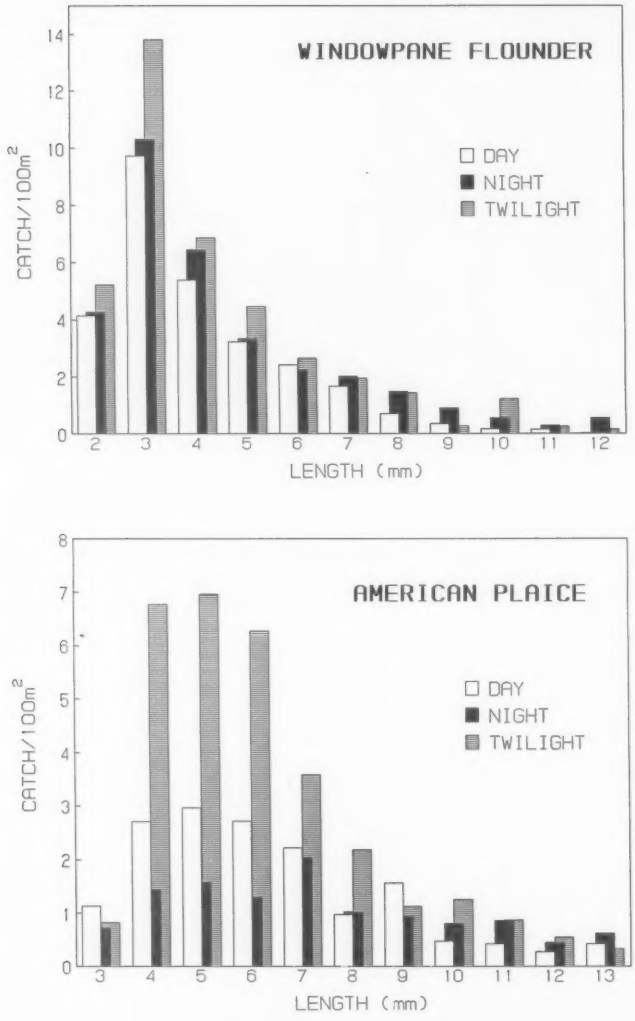
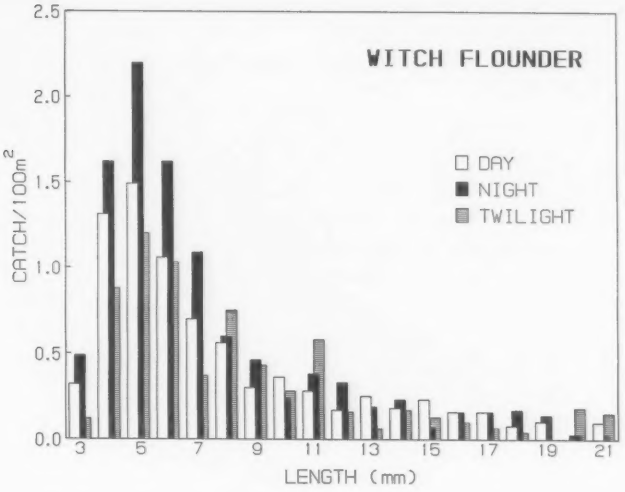
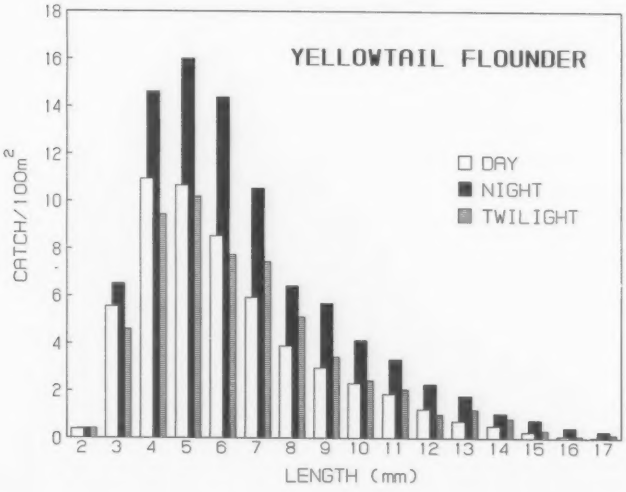


FIGURE 4.—*Continued.*

the haddock. Both butterfish and *B. glaciale* catches are about the same for night and day, regardless of length. Three species show a trend of decreasing ratios of night:day with increasing length with night catches exceeding day catches at the smaller lengths: witch flounder, *Glyptocephalus cynoglossus*; fourspot flounder, *Paralichthys oblongus*; and fourbeard rockling, *Enchelyopus cimbrius*. The last three species, Atlantic cod, *Gadus morhua*; goosefish; and American plaice, *Hippoglossoides platessoides*, have day catches exceeding night catches at the small lengths and as they grow the ratios of night:day equal or exceed one.

If net avoidance by fish larvae is visually cued, the expected ratios of twilight-to-day catches would exceed one and increase with increasing fish length. Another expectation would be that night catches would exceed, on average, twilight catches. As shown in Table 3, 16 of 36 taxa conform to the ranking of night > twilight > day catches. A total of 16 of the 26 taxa analyzed by length (Fig. 4) shows increasing twilight:day catch ratios, determined from expected values from the regression analysis, with increasing length. However, Figure 4 also shows twilight catches often exceeding night catches at some lengths for many taxa. Outstanding examples of dominant twilight catches are offshore hake, American plaice, butterfish, and windowpane flounder, *Scophthalmus aquosus*. The catches of offshore hake show that twilight catches domi-





nate at all lengths (≈ 50% of the total catch) and day catches amount approximately to only 20% of the total. This relationship of catches is unique among the 26 taxa analyzed and is statistically significant ($P < 0.01$, Table 3). Offshore hake larvae occur mostly at the shelf break in depths > 200 m (Morse et al. 1987). Since the maximum water column depth sampled by the net was 200 m, collections of this species may reflect a vertical migration pattern into the net sampling area during twilight as well as visually cued net avoidance.

The catches of *B. glaciale*, *C. maderensis*, Atlantic herring, and rock gunnel, *Pholis gunnelus*, reveal some unique characteristics as analyzed by day, night, and twilight. The length range for *B. glaciale* in Figure 4 is 3–11 mm, but the entire range sampled during this study is from 3 to 52 mm. At 12 mm, the length at which metamorphosis occurs (Halliday 1970), this species is virtually absent from all daylight catches (i.e., 3 individuals > 11 mm in 2,201 tows) though they are abundant, measuring up to about 25 mm long, in both night and twilight tows. Larvae are most abundant at the offshore extreme of the survey area (Morse et al. 1987), and the average bottom depth where they occur is about 400 m while the maximum tow depth is 200 m. Assuming fish begin at metamorphosis, the characteristic vertical migrations of juveniles and adults, this extreme case of net avoidance represents the effect of vertical migration

during the day below the path of the net. Halliday (1970) found the center of distribution during the day is below 450 m (250 fathoms) and at night between 45 and 90 m (25 and 50 fathoms). In contrast to *B. glaciale*, the lanternfish, *C. maderensis*, was captured in all light regimes up to 16 mm. With this species, night catches dominated both day and twilight catches by up to 10 times, but the total length range captured changed little, regardless of light conditions. The length frequencies of Atlantic herring show a distinct polymodality for both day and night catches with peaks occurring at various lengths, depending upon the light regime considered (Fig. 4).

The catches of rock gunnel larvae are the most erratic of the 26 species presented. There appears to be little decrease in abundance with increasing length and they have the lowest ratios of day, night, and twilight catches of any taxa. Figure 4 shows a slight dominance of night catches at the smaller sizes and of twilight catches at the larger sizes. The minimum length (10 mm) corresponds to the large hatching size of rock gunnel and is the largest of any taxa treated here.

Correction Factors

The estimates of the coefficients of the expon-

TABLE 4.—Regression coefficients and mean square error (MSE) for the relationship of mean catch per 100 m^2 United States, 1977–84. Regression constants for the quadratic equation relating the ratios (R) of night:day and the estimate.

	Day			Night			Twilight		
Taxon	*a*	*b*	MSE	*a*	*b*	MSE	*a*	*b*	MSE
Atlantic herring	4.318 (0.478)	−0.290 (0.0293)	0.415	4.306 (0.241)	−0.186 (0.0147)	0.106	5.606 (0.623)	−0.323 (0.0381)	0.703
Ceratoscopelus maderensis	3.150 (0.484)	−0.400 (0.0423)	0.197	4.595 (0.321)	−0.338 (0.0280)	0.086	5.215 (1.043)	−0.504 (0.0912)	0.914
Benthosema glaciale	3.691 (0.334)	−0.404 (0.0405)	0.046	3.790 (0.507)	−0.422 (0.0615)	0.106	2.281 (0.654)	−0.204 (0.0794)	0.176
Goosefish	2.225 (0.308)	−0.383 (0.0323)	0.115	1.769 (0.514)	−0.348 (0.0539)	0.320	1.268 (0.573)	−0.299 (0.0600)	0.396
Urophycis spp.	4.602 (0.383)	−0.410 (0.0334)	0.379	4.828 (0.355)	−0.371 (0.0310)	0.326	4.488 (0.394)	−0.321 (0.0344)	0.402
Fourbeard rockling	2.809 (0.332)	−0.600 (0.0445)	0.119	2.688 (0.181)	−0.550 (0.0243)	0.035	1.193 (0.622)	−0.310 (0.0834)	0.417
Atlantic cod	3.185 (0.118)	−0.307 (0.0091)	0.034	2.423 (0.212)	−0.233 (0.0163)	0.109	1.972 (0.291)	−0.223 (0.0225)	0.206
Haddock	4.887 (0.339)	−0.442 (0.0336)	0.161	5.237 (0.458)	−0.546 (0.0453)	0.293	4.354 (0.333)	−0.418 (0.0329)	0.155
Offshore hake	3.521 (0.531)	−0.653 (0.0770)	0.249	3.384 (0.435)	−0.568 (0.0631)	0.167	4.432 (0.484)	−0.616 (0.0702)	0.207
Silver hake	4.560 (0.217)	−0.357 (0.0151)	0.176	4.195 (0.148)	−0.242 (0.0103)	0.082	4.043 (0.280)	−0.276 (0.0196)	0.294
Bluefish	7.453 (0.412)	−0.947 (0.0526)	0.116	6.260 (0.536)	−0.588 (0.0683)	0.196	6.406 (0.890)	−0.770 (0.113)	0.540
Atlantic croaker	5.974 (0.622)	−0.913 (0.0834)	0.417	4.065 (0.505)	−0.445 (0.0677)	0.275	1.891 (0.379)	−0.379 (0.0508)	0.155
Cunner	5.586 (0.385)	−0.655 (0.0411)	0.101	5.721 (0.279)	−0.497 (0.0298)	0.053	3.978 (0.923)	−0.449 (0.0990)	0.584
Rock gunnel	0.414 (0.707)	−0.106 (0.0355)	0.286	1.072 (0.912)	−0.133 (0.0458)	0.477	−0.253 (1.051)	−0.0712 (0.0527)	0.633
Ammodytes spp.	5.710 (0.104)	−0.223 (0.0050)	0.045	5.926 (0.117)	−0.177 (0.0056)	0.056	5.775 (0.141)	−0.203 (0.0067)	0.081
Atlantic mackerel	7.019 (0.181)	−0.782 (0.0243)	0.035	7.484 (0.432)	−0.701 (0.0579)	0.201	6.583 (0.651)	−0.732 (0.0873)	0.457

ential regression equations fitted to the mean catch per 100 m^2 and to the length for each taxa are shown in Table 4. The regression fitted to twilight catches is often not as accurate as for day or night. This is not surprising because twilight catches represent the transitional time between light and dark regimes when visual avoidance responses to the net are expected to be most variable. This variability is evident in the often high twilight catches at the larger sizes.

The ratios of expected catches calculated from the exponential regressions for night:day and twilight:day catches were fit to polynomial equations and yield corrections for catchability for day, night, and twilight catches (Table 4).

Mortality

Catches of each taxa were corrected for day, night, and twilight catchability, and the mean catch per tow (number/100 m^2) was again calculated for each mm length and the exponential decay model fit to the length frequencies. The slope of the fitted line was used as an estimate of length-dependent mortality (Ebert 1973). Mortalities ranged from 0.114 for rock gunnel to 0.701 for Atlantic mackerel (Table 5). A review of the spawning times of the 26 taxa (Colton et al. 1979; Morse et al. 1987) reveals that 4 of the 6 taxa with the lowest mortalities are winter spawners, and 5 of the 6 taxa with the highest

(C) versus larval length (mm) as $C = a * \exp(\text{length} * b)$ for day, night, and twilight by taxon for larvae caught off the northeast twilight:day mean catches verses larval length (L) where $R = a + b_1 L + b_2 L^2$. Numbers in parenthesis are standard error of

	N/D ratios			T/D ratios		
Taxon	a	b_1	b_2	a	b_1	b_2
Atlantic herring	3.101 (0.260)	−0.325 (0.0360)	0.0287 (0.00115)	3.580 (0.00341)	−0.109 (4.72×10^{-4})	0.00118 (1.51×10^{-5})
Caratoscopelus maderensis	4.572 (0.0372)	0.168 (0.00714)	0.0164 (3.22×10^{-4})	7.146 (0.0530)	−0.576 (0.0102)	0.0140 (4.49×10^{-4})
Benthosema glaciale	1.104 (4.77×10^{-5})	−0.0200 (1.25×10^{-5})	1.59×10^{-4} (7.70×10^{-7})	0.777 (0.0815)	−0.145 (0.0213)	0.0249 (0.00132)
Goosefish	0.637 (0.0815)	0.0209 (0.0213)	5.31×10^{-4} (0.00132)	0.424 (4.45×10^{-4})	0.0173 (1.07×10^{-4})	0.00297 (5.86×10^{-6})
Urophycis spp.	1.266 (0.00204)	0.0437 (4.32×10^{-4})	0.00142 (2.02×10^{-5})	1.061 (0.0296)	0.0181 (0.00630)	0.00909 (2.94×10^{-4})
Fourbeard rockling	0.892 (0.00101)	0.0407 (3.15×10^{-4})	0.00153 (2.22×10^{-5})	1.369 (0.268)	−0.477 (0.0834)	0.0707 (0.00588)
Atlantic cod	0.546 (0.0118)	0.0106 (0.00217)	0.00320 (8.90×10^{-5})	0.380 (0.0126)	3.7×10^{-4} (0.00231)	0.00299 (9.47×10^{-5})
Haddock	1.336 (0.00839)	−0.113 (0.00192)	0.00293 (9.97×10^{-5})	0.588 (1.37×10^{-4})	0.0136 (3.13×10^{-5})	2.09×10^{-4} (1.63×10^{-6})
Offshore hake	0.901 (0.00521)	0.0585 (0.00174)	0.00554 (1.32×10^{-4})	2.491 (8.63×10^{-4})	0.0883 (2.87×10^{-4})	0.00213 (2.18×10^{-5})
Silver hake	1.571 (0.164)	−0.180 (0.0284)	0.0227 (0.00107)	0.765 (0.0292)	−0.00350 (0.00505)	0.00575 (1.90×10^{-4})
Bluefish	8.415 (1.744)	−3.021 (0.495)	0.332 (0.0327)	0.688 (0.0570)	−0.0769 (0.0162)	0.0216 (0.00107)
Atlantic croaker	12.443 (3.420)	−5.265 (1.064)	0.572 (0.0750)	3.331 (0.981)	−1.408 (0.305)	0.146 (0.0215)
Cunner	2.614 (0.217)	−0.314 (0.0509)	0.0610 (0.00280)	1.032 (0.133)	−0.232 (0.0313)	0.0288 (0.00172)
Rock gunnel	1.902 (0.00146)	−0.0472 (1.53×10^{-4})	4.17×10^{-4} (3.93×10^{-6})	0.557 (0.00289)	0.0114 (3.5×10^{-4})	6.35×10^{-4} (7.78×10^{-6})
Ammodytes spp.	1.474 (0.0270)	0.0146 (0.00306)	0.00351 (7.72×10^{-5})	1.080 (0.00130)	0.0204 (1.48×10^{-4})	3.71×10^{-4} (3.73×10^{-6})
Atlantic mackerel	1.648 (0.00987)	0.100 (0.00309)	0.00918 (2.16×10^{-4})	0.651 (7.47×10^{-4})	0.0298 (2.32×10^{-4})	0.00113 1.64×10^{-4})

TABLE 4.—*Continued*

Taxon	Day			Night			Twilight		
	a	*b*	MSE	*a*	*b*	MSE	*a*	*b*	MSE
Butterfish	4.061 (0.332)	−0.479 (0.0362)	0.188	4.226 (0.276)	−0.482 (0.0300)	0.129	4.694 (0.323)	−0.548 (0.0353)	0.178
Sebastes spp.	6.661 (0.363)	−0.738 (0.0418)	0.030	6.415 (0.886)	−0.651 (0.102)	0.183	5.733 (0.395)	−0.606 (0.0455)	0.036
Gulf Stream flounder	4.637 (0.232)	−0.332 (0.0217)	0.086	4.624 (0.168)	−0.274 (0.0157)	0.045	5.524 (0.311)	−0.387 (0.0291)	0.154
Smallmouth flounder	6.088 (0.923)	−0.620 (0.0930)	0.714	4.802 (0.246)	−0.386 (0.0248)	0.051	5.145 (0.610)	−0.555 (0.0615)	0.312
Summer flounder	3.624 (0.271)	−0.516 (0.0315)	0.109	3.655 (0.378)	−0.481 (0.0439)	0.212	3.279 (0.517)	−0.468 (0.0601)	0.398
Fourspot flounder	4.218 (0.175)	−0.396 (0.0161)	0.072	4.635 (0.266)	−0.440 (0.0244)	0.166	3.514 (0.347)	−0.311 (0.0320)	0.287
Windowpane flounder	4.361 (0.361)	−0.612 (0.0450)	0.167	3.212 (0.261)	−0.365 (0.0325)	0.087	3.864 (0.449)	−0.466 (0.0560)	0.258
American plaice	2.460 (0.355)	−0.282 (0.0395)	0.129	1.117 (0.238)	−0.129 (0.0266)	0.058	3.650 (0.216)	−0.356 (0.0240)	0.048
Witch flounder	0.636 (0.220)	−0.153 (0.0158)	0.102	1.497 (0.329)	−0.222 (0.0237)	0.229	0.423 (0.446)	−0.148 (0.0321)	0.421
Yellowtail flounder	4.841 (0.323)	−0.421 (0.0278)	0.141	4.656 (0.140)	−0.331 (0.0120)	0.026	4.557 (0.337)	−0.376 (0.0290)	0.153

TABLE 5.—A list by taxa of the mean surface water temperature (T) of larval fish samples, the instantaneous growth rate (G_w), the minimum length (L_n) and maximum length (L_m) used in the analysis, the days (t) between L_n and L_m, and the instantaneous length (Z_l) and daily (Z_t) mortality rates.

Taxon	T (°C)	G_w	L_n (mm)	L_m (mm)	t (d)	Z_l	Z_t
Atlantic herring	10.5	0.134	7	24	38.16	0.196	0.0873
C. macerensis	19.9	0.269	6	16	15.13	0.338	0.223
B. glaciale	12.4	0.161	5	11	20.32	0.161	0.0780
Goosefish	19.3	0.261	4	14	19.92	0.366	0.261
Urophycis spp.	20.0	0.271	3	18	27.44	0.330	0.180
Fourbeard rockling	15.6	0.207	4	11	26.05	0.399	0.123
Atlantic cod	5.8	0.0661	4	20	101.20	0.259	0.0409
Haddock	6.5	0.0762	4	15	72.17	0.442	0.0674
Offshore hake	16.4	0.219	3	10	22.83	0.616	0.189
Silver hake	17.0	0.227	3	23	37.24	0.242	0.130
Bluefish	23.3	0.318	4	11	13.20	0.588	0.312
Atlantic croaker	20.5	0.278	3	11	19.40	0.481	0.198
Cunner	20.7	0.281	3	13	14.11	0.497	0.282
Rock gunnel	4.4	0.0459	13	26	62.67	0.114	0.0236
Ammodytes spp.	4.6	0.0488	5	32	157.86	0.177	0.0303
Atlantic mackerel	14.4	0.190	3	11	28.38	0.701	0.198
Butterfish	21.6	0.294	3	14	21.74	0.503	0.255
Sebastes spp.	13.3	0.174	6	11	14.46	0.606	0.225
Gulf Stream flounder	23.2	0.317	5	16	15.23	0.298	0.215
Smallmouth flounder	24.5	0.335	4	13	14.60	0.393	0.242
Summer flounder	15.1	0.200	3	13	30.43	0.481	0.158
Fourspot flounder	21.6	0.294	3	17	24.49	0.359	0.205
Windowpane flounder	16.2	0.216	3	12	26.63	0.403	0.136
American plaice	8.6	0.132	4	13	37.06	0.326	0.0791
Witch flounder	10.0	0.127	5	20	45.30	0.185	0.0612
Yellowtail flounder	13.8	0.181	5	17	28.06	0.331	0.142

Taxon	N/D ratios			T/D ratios		
	a	b_1	b_2	a	b_1	b_2
Butterfish	1.174 (*.*)	−0.00383 (*.*)	6.10×10^{-6} (*.*)	1.847 (0.00378)	−0.116 (9.81×10^{-4})	0.00251 (5.68×10^{-5})
Sebastes spp.	0.868 (0.00959)	0.0376 (0.00232)	0.00619 (1.36×10^{-4})	0.603 (0.0251)	−0.0189 (0.00608)	0.0107 (3.56×10^{-4})
Gulf Stream flounder	1.025 (0.00547)	0.0438 (0.00119)	0.00300 (5.88×10^{-5})	2.394 (0.00367)	−0.120 (7.99×10^{-4})	0.00213 (3.94×10^{-5})
Smallmouth flounder	2.969 (0.460)	−0.771 (0.103)	0.0763 (0.00536)	0.410 (0.00265)	0.0182 (5.73×10^{-4})	0.00152 (2.99×10^{-5})
Summer flounder	1.035 (5.52×10^{-4})	0.0346 (1.52×10^{-4})	8.42×10^{-4} (9.34×10^{-6})	0.715 (0.00106)	0.0309 (2.93×10^{-4})	0.00119 (1.80×10^{-5})
Fourspot flounder	1.508 (0.00136)	−0.0623 (3.03×10^{-4})	9.47×10^{-4} (1.49×10^{-5})	0.562 (0.0119)	0.0164 (0.00264)	0.00429 (1.30×10^{-4})
Windowpane flounder	1.527 (0.266)	−0.452 (0.0778)	0.0688 (0.00511)	0.854 (0.471)	−0.0232 (0.0137)	0.0203 (9.03×10^{-4})
American plaice	0.479 (0.0363)	−0.0424 (0.00920)	0.0116 (5.35×10^{-4})	3.222 (0.00740)	−0.214 (0.00187)	0.00484 (1.09×10^{-4})
Witch flounder	2.256 (0.00962)	−0.130 (0.00161)	0.00235 (6.12×10^{-5})	0.808 (*.*)	0.00429 (*.*)	1.23×10^{-5} (*.*)
Yellowtail flounder	1.061 (0.0310)	0.00562 (0.00606)	0.00905 (2.72×10^{-4})	0.770 (0.00207)	0.0282 (4.04×10^{-4})	0.00121 (1.82×10^{-5})

mortalities are summer spawners. The relationship of spawning time and mortality was investigated by calculating the weighted mean surface temperature for each taxa and plotting it against mortality (Fig. 5). Two linear regression lines are fitted to the data points: one for all the data (n = 26); and another without haddock, *Sebastes* spp., offshore hake, and Atlantic mackerel,

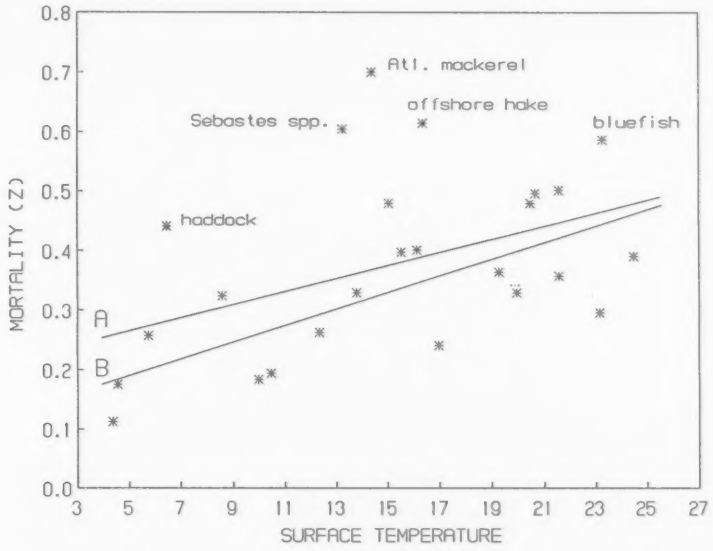


FIGURE 5.—Estimated length-dependent mortality versus mean surface water temperature for 26 larval fish taxa, 1977–84 (curve A, n = 26). Labeled points, except bluefish, were excluded from curve B, n = 22.

(those with the highest mortality (n = 22)). The correlations are significant for both data sets (P = 0.023 for n = 26 and P = 0.001 for n = 22) where r^2 = 0.20 and 0.51, respectively.

DISCUSSION

Net Avoidance

The correction of combined catches of all larvae presents a complex problem because of the interaction of the changes in catchability with the light regime, differential catchability with larval length, and the species composition of catches. The light regime and larval length appear to interact with the catches nonlinearly, as evidenced by the curvilinearity of the relationships of the ratios of night:day catches and larval length. The species composition of the catches represent an amalgam of the differing catchabilities of each taxa. This is illustrated in the catches by depth. Here the changing species composition with depth can be seen to change the ratios of day, night, and twilight catches. The correction for catchability on a station-by-station basis would require individual correction factors for each species in order to correct the entire survey catch. The correction factors presented here allow approximately 90% of all larvae, by numbers, to be corrected for light regime and larval-length catchability interactions.

Much has been written about net avoidance by fish larvae and the need to model length- and gear-dependent net avoidance (e.g., Clutter and Anraku 1968; Murphy and Clutter 1972; Barkley 1972; Ware and Lambert 1985). The models relate reaction distance, i.e., the distance between the net and larva when the net is first detected by the larva, larval swimming speeds, and net characteristics. The theories assume that, if a larva can detect the approaching net and produce sufficient swimming speed relative to net speed, it will avoid capture. This assumption seems unrealistic when compared with catchability using other types of gear. For example, if detection factors and swimming speed of fishes were applied to bottom trawls instead of plankton gear, it is clear that very few species of adult fishes would be captured. Catchability obviously involves numerous factors, and Barkley (1972) concluded that the application of net avoidance theory requires detailed knowledge of larval behavior, and net design and its fishing characteristics.

Corrections for day, night, and twilight catchability are not intended to account for all net avoidance by larvae. These corrections are intended to standardize the abundance of larvae from net catches, regardless of the light conditions. Obviously, net avoidance may and probably does occur (see Murphy and Clutter 1972), regardless of the light conditions, but before the application of theoretical corrections for net avoidance are attempted, it is appropriate to standardize the catches. Changes in catchability with varying light conditions and larval length are clearly demonstrated from this study. Many of the taxa show the expected relationship, if visual detection of the net is the primary cue for net avoidance, of night > twilight > day catches. Night:day catch ratios exceeding one are reported for a variety of gears and taxa (Alhstrom 1954; Bridger 1956; Richards and Kendall 1973; Lenarz 1973; Lough et al. 1982; Potter and Lough 1987; etc.). However, the dominance of twilight catches for Gulf Stream flounder, butterfish, American plaice, and offshore hake reveals a more complex nature for net avoidance and the need for species-specific studies as they relate to gear avoidance. It is difficult to speculate what behavioral mechanism is producing the increased twilight catches for these taxa, but perhaps light intensity within the water column and feeding behavior may be interacting to increase catchability of these larvae. A study of gut fullness and catchability, i.e., decreased mobility of larvae with full guts, could reveal a relationship between feeding, light intensity, and catchability.

Bimodal or polymodal length frequencies of Atlantic herring larvae appear common in field samples (e.g., Saila Lambert 1984 and Lough 1981), and are attributed to successive hatchings of larvae into the plankton community. It is unlikely that the combined-years' length frequencies in Figure 4 could reveal cohorts as described by Lambert (1984). A close look at the catches of larvae show day catches have just two or perhaps three modes and night catches have at least five modes while twilight catches have at most two modes. The combined length frequency of all larvae captured, regardless of hour of capture, is unimodal at 7 mm. At this point it is difficult to speculate on the causes of different polymodal length frequencies for day and night catches, but future studies of Atlantic herring larval abundance should be done cautiously when examining length-frequency curves.

Mortality and Growth

Survey timing has a profound effect on the mortality estimates from either length- or age-frequency curves. This is most evident if samples are not taken systematically during the spawning season and surveys are not timed and spaced evenly along the spawning curve (Hewitt and Methot 1982; Morse and Hauser 1985; Hauser et al. 1988). Mortality is overestimated from samples taken when spawning or larval production is increasing and underestimated when spawning is decreasing. The magnitude of the bias in mortality estimation shows a twofold to threefold decrease with samples from the beginning to the end of spawning. However, if survey samples are summed over the larval production cycle and at least four surveys are spaced evenly throughout the spawning cycle, the over- and underestimates cancel out and the combined data give a good estimate of mortality (Hewitt and Methot 1982). The process of combining surveys across years increases the number of samples taken during the spawning cycle from approximately 2 to 5 for each year to an observation every 4 to 10 days during the combined production cycle for each taxa. The result of this process is the calculation of an average length-dependant larval mortality for the eight years covered by this study.

The relationship of larval mortality and water temperature has some interesting implications about larval growth rates. Mortality, as an expression of the decrease in numbers over time by substituting time (t_i) for length (X_i) in Equation 2, is directly related to larval growth rate by the term t_i. The assumption is that, as fish larvae grow, mortality rate decreases (Ware 1975). With constant predation rates, the amount of time spent at a given size, commonly referred to as "stage duration", will determine the number of surviving larvae. The implication of this relationship of growth rate and mortality is that, owing as water temperature increases, stage duration will decrease to increased growth rate and the shorter stage duration will decrease mortality. This assumes that adequate food supplies are available for the increased metabolic demands of increased growth rates. The link between "stage duration" and particle-size dependent mortality rates would appear to be valid for most pelagic fish larvae given the rather small size range of newly hatched fishes. However, if larval mortality rates were, in fact, dependent upon growth rates as outlined above, fishes spawning in warm waters would derive a significant survival advantage over cold water spawners and mortality would be inversely correlated with growth rates.

According to population dynamics theory, mortality and growth rates must be positively correlated with the ratio of the instantaneous growth rate to instantaneous mortality rate, averaging > 1 for the biomass of a cohort of fish to increase (Beverton and Holt 1957; Ricker 1975; Ware 1975). If this were not the case, the maximum biomass of a cohort would occur at the egg stage. The results presented here (Fig. 5) show that length-dependent larval mortality is positively correlated with mean surface water temperature, and it seems clear that estimated mortalities are higher in the warm-water months than during winter. The association of temperature and larval growth rate was determined from a review of laboratory studies of larval growth rates (Table 6). The relationship of increasing growth rate with increasing temperature is not surprising, but the high coefficient of determination (93%) is surprising, given the variety of experimental procedures, prey species, densities, and fish species utilized by the experimenters. The data in Table 6 and the relationship of temperature to mortality confirm the positive correlation of growth and mortality.

Because expected ratios of instantaneous growth and mortality rates have been shown to be temperature-dependent, either rate is easily determined if the other is known. This ability to calculate either rate would have direct applications in modeling larval fish populations as it relates to survivorship, predator-prey dynamics, and the expected effect of environmental temperatures. For this study, if growth rate is known, then the mortality rates from field samples could be investigated to determine if net avoidance is a serious bias as often speculated. Growth rates in weight in Table 6 are rates per day, but mortalities in Figure 5 are rates per mm length interval. To convert lengths to ages (t = days), the length (mm) to weight (μg), relationship and instantaneous growth rate are dimensioned in days and μg where

$$\text{Weight} = c * \text{Length}^b$$

and the instantaneous growth rate (G_n)

$$G_w = (\ln W_{i+1} - \ln W_i)/(t_{i+1} - t_i)\,.$$

Thus

TABLE 6.—Listing of instantaneous larval growth rates per day and water temperatures (°C) from laboratory growth studies and linear regression analysis.

Species	Temp.	Growth	Source
Atlantic cod, *Gadus morhua*	4	0.0424	Laurence 1978
	7	0.0762	Laurence 1978
	10	0.0916	Laurence 1978
Haddock, *Melanogrammus aeglefinus*	4	0.0375	Laurence 1978
	7	0.0569	Laurence 1978
	9	0.1434	Laurence 1978
	6	0.0408	Buckley et al. 1987
	6	0.0367	Buckley et al. 1987
Sand lance, *Ammodytes* spp.	6	0.0877	Buckley et al. 1987
	6	0.0845	Buckley et at. 1987
	8	0.1065	Buckley et al. 1987
Atlantic mackerel, *Scomber scombrus*	15	0.1755	Buckley et al. 1987
	15	0.1948	Buckley et al. 1987
Pacific mackerel, *Scomber japonicus*	19	0.3383	Hunter and Kimbrell 1980
Atlantic herring, *Clupea harengus*	8	0.1165	Checkley 1984
Winter flounder, *Pseudopleuronectes americanus*	2	0.0263	Laurence 1975
	5	0.0598	Laurence 1975
	8	0.1065	Laurence 1975
Walleye pollock, *Theragra chalcogramma*	9.3	0.1031	Bailey and Stehr 1986
Bay anchovy, *Anchoa mitchilli*	26	0.3439	Houde and Schekter 1981
Sea bream, *Archosargus rhomboidalis*	26	0.4050	Houde and Schekter 1981
Lined sole, *Achirus lineatus*	28	0.3257	Houde and Schekter 1981

Linear Regression Analysis of growth rate (Y) on temperature (X):
$Y = a + bX$ $a = -0.0174$ $b = 0.0144$ $S_{Y.X} = 0.0314$ $r^2 = 0.928$.

$$t_{i+1} - t_i = b(\ln L_{i+1} - \ln L_i)/G_w .$$

Then Z_t, the instantaneous mortality rate per day, where $t_{i+1} - t_i$ equals one day, is calculated as

$$-Z_t = (\ln N_0 - \ln N_t)/t$$

based on

$$N_t = N_0 e^{-Zt}$$

where N_0 is number at L_0 and N_t, adjusted for stage duration, is number at L_t. G_w for each species was estimated from the growth rate – temperature relationship in Table 6. The length-weight exponent (b) was estimated as the mean regression coefficient for seven species in Laurence (1979) at 4.15 (SE = 0.14). G_w and Z_t were calculated for 26 taxa and are shown in Table 5. The equation relating mortality (Z_t) to temperature (T) is

$$Z_t = -0.2722 + 0.01015\ \mathrm{T}$$

$$r^2 = 0.80 \quad S_{Y.X} = 0.0380.$$

As mentioned above, the ratio of growth rate to mortality rate must exceed one and as Ware (1975) estimated from three data points, the ratio of mortality to growth is near 0.7. The slope of the linear regression for the species in Table 5 is 0.820. Five taxa are near or greater then a ratio of one (i.e., mortality ≥ growth): Atlantic mackerel, *Sebastes* spp., haddock, cunner, and bluefish (Fig. 6). The mortality rates calculated for these taxa are suspect and may represent excessive net avoidance by the larger larvae. When these taxa are eliminated from the data the slope is 0.760 (SE = 0.051, n = 22). The

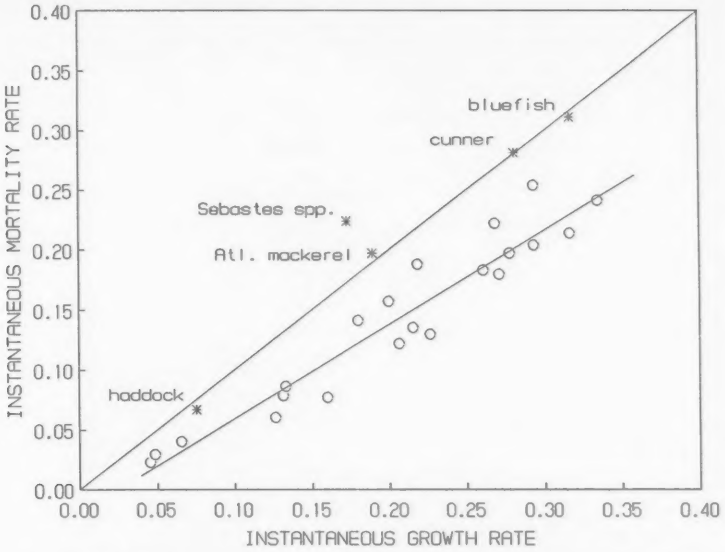


FIGURE 6—Plot of instantaneous larval mortality rates versus instantaneous growth rates for 26 larval fish taxa, 1977–84. Labeled points (n = 5) were excluded from the fitted curve.

ratios of mortality to growth coefficients for the rest of the taxa appear to be reasonable, i.e., approximately 0.7–0.8, and indicate that net avoidance is not a serious problem. It is interesting to note that the relationships of temperature- and length-dependent mortality (Fig. 5) showed that Atlantic mackerel, haddock, bluefish, and *Sebastes* spp. exhibit high mortality rates relative to the temperature, which lends support to the conclusion that net avoidance is the primary factor producing high mortality estimates. Offshore hake also shows a high mortality versus temperature, but does not exceed a ratio of one in the mortality versus growth rate plot. It is unclear which factor, temperature, net avoidance, mortality estimation, or a combination, is the dominant factor affecting the offshore hake data.

Contrary to this analysis, Houde (1989) found from a literature review of larval growth and mortality rates that mortality exceeded growth by about 40–100% over a temperature range of 5°–30°C. The relationship of growth to mortality during the larval stage has important implications about the life history dynamics during the first year of life. For example, when the expected growth and mortality rates at 10°C from Houde's study and this study are applied to 10^6 newly hatched larvae (weighing 0.05 mg each) until metamorphosis (38.2 mg), quite different results are found.

	Z_t	G_w	*Larval stage (d)*	*Metamorphosis* No.	*Metamorphosis* Weight (g)
This study	0.094	0.1266	59.09	3,799	145.12
Houde (1989)	0.1486	0.0904	80.11	7	0.26

The 3–4 orders of magnitude difference in numbers and weight at metamorphosis between the two studies indicate that the growth and mortality rates during the juvenile stage must be very different for recruitment to be successful. If the biomass of a year-class declines during the larval stage, as indicated by Houde (1989), then the ratio of growth to mortality must be high during the juvenile stage. Since growth rate tends to decline during the juvenile stage (Cushing 1975), compared to the larval stage, then mortality of the juvenile stage must be very low.

The close interdependence of larval growth and mortality rates on temperature is clearly demonstrated in this study. It is important to realize that these results represent average conditions for larvae during the eight years from 1977 to 1984. The average values for mortality, growth, and temperature form a baseline against which areal, seasonal, or annual variations in these important early life history parameters can be compared. Thus hypotheses about larval

growth or mortality can be quantitatively tested for significant deviations from the average expected values presented here. In addition, catchability of fish larvae by various plankton samplers can be compared with the expected mortality to determine serious biases.

The three major hypotheses suggested as mechanisms that control survival of larval fishes are starvation, predation, and advection into unfavorable environments. Clearly, advection is a special case which differs little from predation in its effects on the larval population and may be viewed as simply an abiotic "predator". The predator-prey interactions in the pelagic ecosystem may then be partitioned, in terms of mortality, into starvation and predation. It is often not clear whether larvae actually die from lack of adequate food supplies or become more vulnerable to predation as a result of starvation. In any case, larval mortality increases with increasing temperature, thus a major and consistent agent of mortality must be associated with water temperature. If the assumptions of size-dependent mortality, as explained by the "cube root rule", are valid, and there is no reason to reject them, predation rates on larvae must be the primary agent of mortality. Since metabolic rates increase with temperature ($Q_{10} \approx 2$–3; Hoar 1966), predator consumption rate would also increase. Thus increased growth due to increases in temperature would appear to impart no advantage to reduce larval mortality because of the concomitant increase in consumption rates of the predator field. Pauly's (1980) conclusions for juvenile and adult fishes support this hypothesis. An interesting consequence of this hypothesis is that, within the pelagic ecosystem, mortality rates will change with temperature without altering the predator field. Thus investigations of predator-prey interactions must account for the confounding effects of temperature on growth, consumption, and mortality.

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It is an honor to submit this contribution in dedication to Dr. Reuben Lasker, a pioneer in the study of early life history dynamics of fishes. His insight into the oceanic processes affecting larval fish survival has provided inspiration for this study.

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A Method for Correcting Catches of Fish Larvae For the Size Selection of Plankton Nets

David A. Somerton and Donald R. Kobayashi

ABSTRACT: Length distributions of fish larvae obtained with plankton nets are usually biased because large larvae avoid the net and small larvae are extruded through the meshes. Such bias is often corrected by determining the ratio between a standard net and a test net with either zero extrusion or zero avoidance. However, when avoidance of the test net with zero extrusion or when extrusion through test net with zero avoidance differs from the standard net, then the usual method of correcting for size selection results in biased estimates. For such situations, we propose a method that explicitly considers both differential extrusion and differential avoidance and that provides estimates of variance for the corrected length-frequency distributions. The method was applied to length-frequency data for the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. It was shown that a 1 m plankton net with 0.335 mm mesh dropped vertically through the water column during the day effectively samples nehu larvae only between 2.25 and 6.75 mm, roughly one-third of the total length range.

For many aspects of larval fish ecology, accurate estimates of length distribution are imperative, yet the length distribution of larvae obtained with a plankton net is nearly always biased because large larvae avoid the net and small larvae are extruded through the meshes. Previous research on methods to correct larval catches for such size selection has focused on either extrusion (Lenarz 1972) or avoidance (Barkley 1972; Murphy and Clutter 1972), implicitly assuming that the two aspects of size selection are independent. Although this assumption seems reasonable, situations arise in which the problems of estimating extrusion and avoidance are unavoidably linked.

Nearly all empirical or analytical studies of avoidance and extrusion are based on the premise that the number of larvae captured by a plankton net (N_o) is proportional to the number originally in the path of the net (N):

$$N_o = P_c\, N\,, \tag{1}$$

where the proportionality constant (P_c) varies with larval length. P_c can be considered as the probability of capturing a larva, and this, in turn, can be considered as a product of an entry probability (P_e) and a retention probability (P_r):

$$P_c = P_e\, P_r\,; \tag{2}$$

where P_e is equal to 1 minus the probability of a larva avoiding the net and P_r is equal to 1 minus the probability of a larva being extruded through the meshes, given that it has entered the net.

Since an estimator for N can be obtained by combining and rearranging the above equations,

$$N = \frac{N_o}{P_e\, P}\,, \tag{3}$$

the problem of correcting for size selectivity is one of estimating P_e and P_r for each length interval.

To estimate P_e or P_r, catches of a standard net are usually compared with those obtained by some test net used to sample the same population of larvae. In this paper, we will refer to these comparisons as either entry or retention experiments. Assuming catches are standardized to reflect equal filtration volumes, the general form of a net comparison is

$$\frac{N_{os}}{P_{es}\, P_{rs}} = \frac{N_{oi}}{P_{ei}\, P_{ri}} = N\,, \tag{4}$$

where the second subscript refers to the standard net (s) and to the test net used in either an entry experiment ($i = e$) or a retention experiment ($i = r$). Expressed in words, Equation (4) states that the corrected catches from the standard and test nets are both unbiased estimates of the true abundance of larvae and are therefore equal.

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For an entry experiment, an appropriate test net is one that has no larval avoidance (i.e., $P_{ee} = 1.0$) over the size range of interest. After substituting this value for the entry probability and rearranging terms, Equation (4) can be expressed as

$$\frac{N_{os}}{N_{oe}} = \frac{P_{rs}}{P_{re}} P_{es} . \quad (5)$$

Likewise, for a retention experiment, an appropriate test net is one that has no larval extrusion (i.e., $P_{rr} = 1.0$). After substituting this value for the retention probability and rearranging terms, Equation (4) can be expressed as

$$\frac{N_{os}}{N_{or}} = \frac{P_{es}}{P_{er}} P_{rs} . \quad (6)$$

To simplify Equations (5) and (6) further, previous studies have assumed that either the larval retention of the test net used in an entry experiment was identical to that of the standard net (i.e., $P_{rs} = P_{re}$; Barkley 1972; Murphy and Clutter 1972) or that the larval entry into the test net used in a retention experiment was identical to that of the standard net (i.e., $P_{es} = P_{er}$; Lenarz 1972; Colton et al. 1980; Leak and Houde 1987). With these assumptions, Equations (5) and (6) become

$$\frac{N_{os}}{N_{oe}} = P_{es} , \quad (7)$$

and

$$\frac{N_{os}}{N_{or}} = P_{rs} . \quad (8)$$

In other words, entry and retention probabilities of the standard net were estimated as the ratio of the catches of the standard and test nets within each length interval.

When neither assumption can be made, the estimation procedure is complicated in two ways: First, P_{es} and P_{rs} cannot be estimated as simple ratios of the catches of the standard and test nets because they additionally depend on other unknown entry and retention probabilities. This means that P_{es} and P_{rs} cannot be estimated independently for each length interval and must instead be expressed as functional relationships of larval length and estimated simultaneously for all size intervals. Second, the equations for the entry experiment, Equation (5), and the retention experiment, Equation (6), contain both P_{es} and P_{rs}; therefore, the two probabilities are confounded and must be estimated jointly.

In this paper, a method is described for estimating the entry and retention probabilities for this more difficult situation, and this method is then applied to correct the length-frequency distribution of larval Hawaiian anchovy or nehu, *Encrasicholina purpurea*, obtained with plankton nets.

MATERIALS AND METHODS

The standard plankton net that we used to sample eggs and larvae of nehu was constructed of 0.335 mm Nitex[1] and measured 1 m in diameter and 5 m long. The net was not towed but deployed instead by our allowing it to drop vertically through the water column until it hit the bottom, then retrieved with a line attached to a choke collar surrounding the mesh approximately 15 cm from the mouth of the net.

Retention and entry experiments were conducted on 28 March 1988 within Pearl Harbor, HI. The retention experiment consisted of 10 paired net drops, in which the standard net and a test net were deployed simultaneously at one location during daylight hours when the standard net was normally used. The test net was identical to the standard net in all dimensions, but it had a smaller mesh size (0.183 mm). The entry experiment was conducted at each of three nearby (<0.5 km distance) locations and consisted of five deployments of the standard net during the day and five deployments of the same net the following night at each location. Since sampling could not be paired in this experiment, we were concerned that patchiness and horizontal movement of fish by tidal currents might alter the length distribution between day and night sampling. To reduce this, the sampling locations chosen had weak tidal currents, and in addition, sampling was partitioned between three locations rather than concentrated at one. Water depth at all sampling locations was approximately 12 m. The sample obtained from each deployment of each net was stored separately in 10% buffered formalin.

During the retention experiment, the test net

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

appeared to become clogged with algae despite efforts to clean it between deployments. To determine whether the test net was indeed clogged and filtered less water than the standard net, we assumed filtration volume was proportional to the catch of nehu eggs and used a paired t-test to compare egg catches between nets. The test net caught significantly fewer eggs ($P < 0.05$); therefore, the test net was assumed to have filtered less water. To correct for the difference in filtration volume, larval catches in the test net were multiplied by the ratio of the egg catch of the standard net to that of the test net in each pair of deployments.

Nehu larvae were subsequently measured to the nearest 0.1 mm by using a video digitizing system (Optical Pattern Recognition System produced by Biosonics, Inc., Seattle, WA). For preflexion and early flexion larvae, length was measured from the snout to the end of the notochord. For larvae with fully formed tails, length was measured from the snout to the base of the caudal fin rays. The length distributions were not corrected for shrinkage due to preservation, but since all samples were maintained in preservative for about the same length of time, it is unlikely that shrinkage varied among samples.

The entry and retention probabilities were estimated by simultaneously fitting Equations (5) and (6) to the length-frequency data by using nonlinear regression, but before this could be done, three problems had to be solved. First, the entry and retention probabilities could not be estimated independently for each length interval; therefore, Equations (5) and (6) had to be modified so that the probabilities were expressed as functions of larval length. Retention probabilities were chosen to vary with length as logistic functions and thus have the form $P = 1/(1 + ae^{-bl})$, where a and b are parameters to be estimated and l is larval length (Ricker 1975). Entry probabilities, because they are decreasing functions of length, were chosen to have the form $P = 1 - (1/(1 + a\ e^{-bl}))$. After the logistic functions were substituted for the two entry probabilities (P_{es} and P_{er}) and two retention probabilities (P_{rs} and P_{re}) in Equations (5) and (6), the resulting statistical model had eight parameters.

Second, variability in the catch ratio changed with larval length, owing to the change in sample size, and necessitated the use of weighting factors in the regressions (Draper and Smith 1981). The weighting factors used were equal to $1/\text{var}(N_{os}/N_{oi})$, where *var* is the variance and N_{oi} can be either N_{or} or N_{oe}. Variance of the catch ratio was approximated by using the delta method (Seber 1973):

$$\text{var}(N_{os}/N_{oi}) = (1/N_{oi})^2\ \text{var}(N_{os}) + (N_{os}/N_{oi}^2)^2\ \text{var}(N_{oi}) - 2\ (N_{os}/N_{oi}^3)\ \text{cov}(N_{os},N_{oi})\ , \quad (9)$$

where cov indicates covariance. The number of larvae captured in each length class (N_o) was assumed to vary as a multinomial random variable. The variance of N_o was therefore expressed as $N_\bullet P(1 - P)$; where N_o is either N_{os}, N_{or} or N_{oe}; $N_\bullet$ is the sum of N_o over all length intervals; and $P = N_o/N_\bullet$. Although the covariance between the catches of the standard and test nets could be estimated for the retention experiment, it could not be estimated for the entry experiment because sampling was not conducted pairwise. However, the covariance term for the retention experiment was, for all size intervals, approximately 100 times less than the sum of the two variance terms (Equation (9)). On this basis, we assumed that the covariance term was generally small and could be ignored in both the entry and retention experiments.

Third, since the catch ratios fluctuated widely and often became infinite in the larger length intervals where sample sizes were small, the length distributions were truncated prior to fitting the equations. For the entry experiment, truncation occurred at the smallest length interval with zero catch by the test net. For the retention experiment, however, this rule resulted in an extremely narrow length range because the catches obtained with the test net were zero at relatively small lengths. To circumvent this problem, the inverse of Equation (5) was fit to the data, and truncation occurred at the smallest interval with zero catch by the standard net. Weights were calculated by using Equation (9) after substituting N_{os} for N_{oi} and vice versa.

Once Equations (5) and (6) had been fit to the data, the values P_{rs}, P_{re}, P_{es}, and P_{er} were estimated by evaluating the logistic functions at each 0.5 mm length interval using the parameter estimates. P_c for the standard net was calculated for each length interval as the product of the estimates of P_{es} and P_{rs}. Length-frequency data from nehu larvae were then corrected for extru-

sion and avoidance by dividing each N_o by the estimated value of P_c for the appropriate length interval. To better visualize the effect of this correction, we chose N_o from a data set that was considerably larger (N = 4,178) than those used in the net comparisons because histograms of this larger data set were smoother in appearance. This larger data set comprises all larvae that we have measured to date (including those obtained in the net comparisons) and that were collected during the day by the standard net.

The variance of the estimated value of N was approximated by using bootstrapping (Efron and Gong 1983): 1) each of the four experimental length-frequency data sets was randomly subsampled with replacement to produce four new samples with the same sample sizes as the originals; 2) Equations (5) and (6) were fit to the four synthetic samples by the methods described above; 3) P_{es}, P_{er}, P_{rs}, P_{re}, and P_c were estimated for each length interval; and 4) N for each length interval was estimated by dividing the N_o from the large sample of nehu length-frequency data by the estimated value of P_c. This procedure was repeated 500 times, generating 500 independent estimates of P_c for each length. To reduce variance owing to rare but extremely large estimates of N produced when P_c was near 0, the data were trimmed by eliminating the 25 largest estimates within each length interval (5% of the sample). After data trimming, the variance was calculated among the remaining 475 independent estimates.

The variances of P_{es}, P_{er}, P_{rs}, and P_{re} were also calculated from the same 500 independent estimates (no data trimming was required). A two-sample t-test incorporating these variances was then used to test for significant differences between P_{es} and P_{er} and between P_{rs} and P_{re} within each length interval.

RESULTS AND DISCUSSION

The estimated entry probabilities for the standard net (P_{es}) decreased from 1.00 for 3 mm larvae to near 0.00 for 10 mm larvae, whereas the entry probabilities for the small mesh net (P_{er}) decreased from 0.95 for 3 mm larvae to near 0.00 for 8 mm larvae (Fig. 1). When the apparent difference in entry probabilities between the two nets was examined statistically for each 0.5 mm length interval between 2.5 and 10.75 mm, P_{er} was found to be significantly less than P_{es} (two-sample, one-tailed t-test; $P < 0.05$) for all length

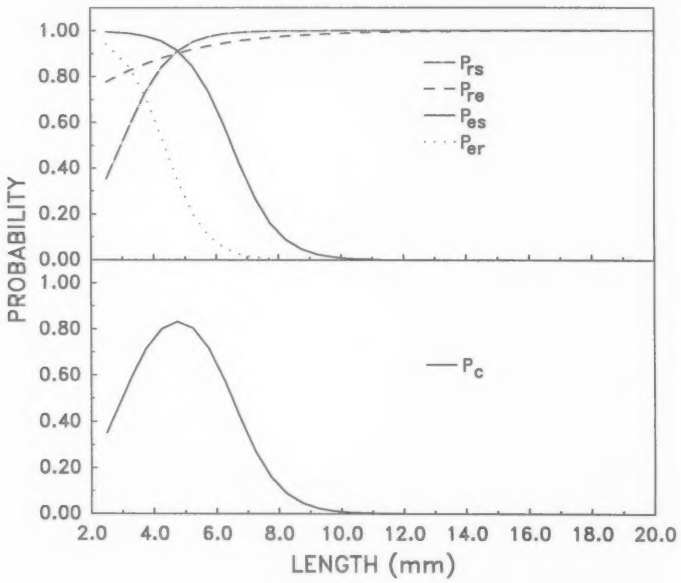

FIGURE 1.—Entry probabilities for the standard (P_{es}) and test nets (P_{er}) and retention probabilities for the standard (P_{rs}) and test nets (P_{re}) are shown by 0.5 mm length intervals (upper panel). Capture probability (P_c) for the standard net is shown by 0.5 mm length interval (lower panel).

intervals ≥4.25 and ≤6.75 mm. This result is surprising because the two nets were identical except for mesh size which, by itself, is unlikely to influence avoidance. However, the catch of nehu eggs in the test net was significantly less than in the standard net (paired t-test, $P < 0.05$), indicating, to the extent egg catches can be used as a measure of filtration volume, that the test net was likely clogged by abundant filamentous algae in Pearl Harbor during sampling. Such clogging not only decreased the apparent amount of water entering the test net but also may have slowed the sinking rate, allowing larvae to avoid the net more easily.

The estimated retention probabilities for the standard net (P_{rs}) during the day increased from about 0.35 for 2.5 mm larvae to nearly 1.00 for 6.0 mm larvae (Fig. 1). At night, however, the standard net appeared to have higher retention probabilities in the smallest length intervals (P_{re}; Fig. 1). When this difference was examined statistically (two-sample t-test), P_{re} and P_{rs} were not significantly different at $P \leq 0.05$ in any length interval, but they were significantly different at $P \leq 0.15$ within the two smallest length intervals. Although the differences between P_{re} and P_{rs} are relatively small, considering the same net and method of deployment were used during both day and night sampling, it is surprising that any differences were detected. One possible explanation is that the density of small larvae, rather than the retention probability, was higher at night. This could have occurred either because, by chance alone, the density of small larvae was higher in the patches sampled at night or because the mean density was higher as a result of eggs hatching between the day and night sampling. However, the addition of new larvae is unlikely because, at the time of year when our sampling occurred (March), nehu eggs hatch during the morning and new larvae would therefore have been equally available to both our day and night sampling (Clarke 1989). A second explanation is that the greater retention of small larvae at night is real and at least partially due to morphological changes increasing the catchability of larvae between the day and night sampling periods. Evidence for this is weak; however, Clarke (1989) reported that during March nehu larvae display considerable development of their eyes, mouth, and pectoral fins between midday and early evening of their third day of life. Development of such features might increase catchability relative to equal-sized, but undeveloped, larvae.

Regardless of the reasons, over some length ranges, $P_{rs} \neq P_{re}$ in the entry experiment and $P_{es} \neq P_{er}$ in the retention experiment; both cases are violations of the assumptions implicitly made when entry and retention probabilities are estimated as simple catch ratios (i.e., catch of standard net/catch of test net). The effect of ignoring this can be judged from plots of entry and retention probabilities estimated from simple catch ratios and estimates of P_{es} and P_{rs} using our method (Fig. 2). Entry probabilities estimated from simple catch ratios are similar to P_{es} for larvae ≥4.0 mm but are increasingly less than P_{es} at smaller lengths. This region of underestimation corresponds approximately to the length interval in which the retention of larvae differed between day and night (Fig. 1). Retention probabilities estimated from simple catch ratios are similar to P_{rs} at larval lengths <4 and >8 mm, but are considerably larger than P_{rs} at intermediate lengths. Again, this region of overestimation corresponds approximately to the length region in which avoidance differed between the standard and test nets (Fig. 1). Violation of the assumptions therefore leads to bias in estimates of entry and retention probabilities based on simple catch ratios.

The success of a net comparison, however, also depends upon the validity of several other assumptions. Foremost are the assumptions that no avoidance of the test net occurred in the entry experiment ($P_{ee} = 1.0$) and no extrusion through the test net occurred in the retention experiment ($P_{rr} = 1.0$). Violations of these assumptions lead to positive bias in the estimates of P_{es} and P_{rs}. For the entry experiment, P_{ee} was definitely higher than P_{es} over a broad range of sizes because more larvae were caught at night and a sizable fraction of the catch was larger than the largest larva caught during the day (Fig. 3). But no evidence indicates P_{ee} remained equal to 1.0 for size intervals ≤14.0 mm (the size of the largest larvae caught during the day), as is required to obtain unbiased estimates. For the retention experiment, P_{rr} was definitely higher than P_{rs} because more small larvae were captured with the test net (Fig. 3). But, again, no evidence indicates P_{rr} remained equal to 1.0 for size intervals ≥2.00 mm, the smallest size category.

Still another assumption is that, in each of the two experiments, the standard and test nets both sampled the same population of larvae. For the retention experiment, the assumption is certainly valid because the two nets were deployed

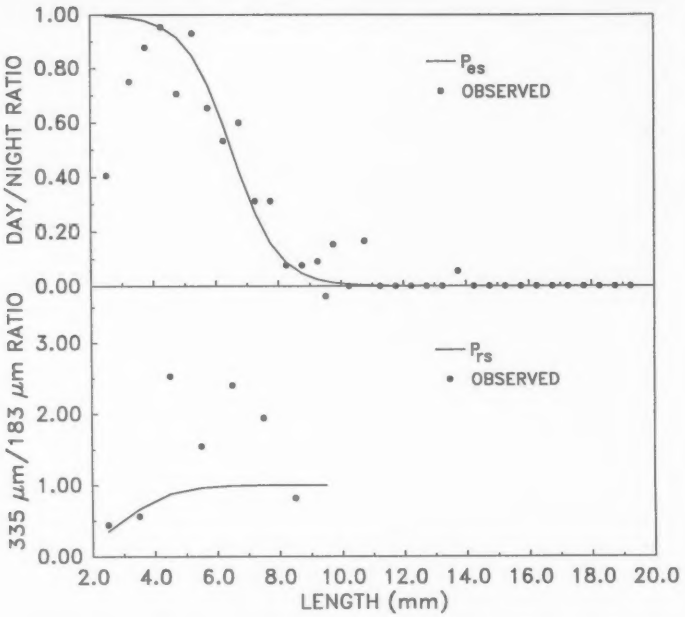

FIGURE 2.—Estimated values of P_{es} and the day to night catch ratio by 0.5 mm length intervals obtained in the avoidance experiment (upper panel). Estimates of P_{rs} and the 0.335 mm standard net to the 0.183 mm test net catch ratio by 1.0 mm length intervals obtained in the extrusion experiment (lower panel).

simultaneously from a small boat. For the entry experiment, however, deployment of one of the nets occurred approximately 10 hours after the other, and any patchiness in the larval distribution coupled with advective movement could have substantially altered the characteristics of the population sampled. We attempted to minimize this problem by increasing the sample size, relative to the retention experiment, and by partitioning the sampling among three locations rather than by concentrating it at one. Sampling variability, however, may still have been responsible for some of the differences between the day and night size distributions. This problem has been encountered in other studies using day and night comparisons to estimate entry probabilities (Murphy and Clutter 1972), and the only effective solution is increased sample sizes.

Since the method of estimating entry and retention probabilities proposed here requires more effort than that using simple catch ratios, it is important to determine at the outset whether the assumptions that $P_{rs} = P_{re}$ and $P_{es} = P_{er}$ have been violated so that the appropriate method of analysis can be chosen. Some indication of the validity of these assumptions can be obtained by examining plots of catch ratios as a function of larval length (Fig. 2). Two cases are evident in our data. First, if the assumptions are met, catch ratio should be a monotonically increasing or decreasing function of larval length because extrusion and avoidance are monotonic functions of larval length. This is not true in the avoidance experiment where the catch ratios increased for lengths ≤4 mm and decreased thereafter. Second, if the assumptions are met, catch ratios cannot be >1.0, because, except by chance alone, catch in the standard net is less than the catch in the test net. This is not true for the extrusion experiment where the catch ratios in some length intervals are >2.0. If either of these conditions are evident in plots of catch ratios, the method of estimating entry and retention probabilities proposed here is preferable to simple catch ratios.

Although we considered the problem in which both $P_{rs} \neq P_{re}$ and $P_{es} \neq P_{er}$, this is the most general of several related problems that could be approached with slight variations in our methodology. One example occurs when either $P_{rs} \neq P_{re}$ or $P_{es} \neq P_{er}$ but not both. In this case, either

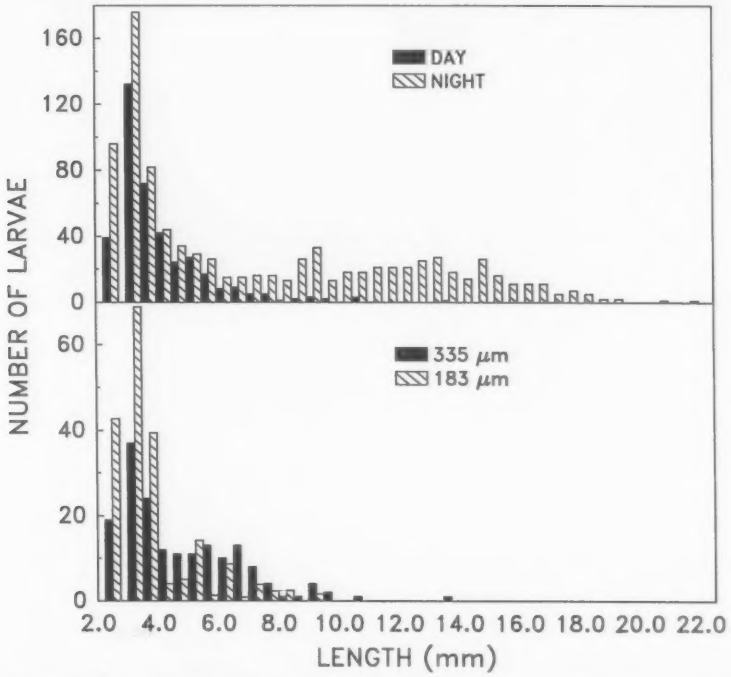

FIGURE 3.—The number of larvae by 0.5 mm length intervals captured in Pearl Harbor, HI, in March 1988. The entry experiment (upper panel) used a 0.335 mm standard mesh net during the day and night. The retention experiment (lower panel) used both a 0.183 mm mesh test net and a 0.335 mm standard mesh net during the day.

Equation (5) or (6) could be simplified by deleting either P_{rs}/P_{re} or P_{es}/P_{er}, but parameter estimation would still require a simultaneous fit of the two equations to the catch ratios. A second example occurs when only an entry experiment or retention experiment is conducted and the appropriate assumption is violated. In this case, the entry and retention probabilities still must be expressed as functions of larval length, thus requiring that nonlinear regression be used to fit either Equation (5) or (6) to the catch ratios.

The efficacy of the standard net at sampling nehu larvae can be judged in two ways. First, it can be judged by the length range sampled with a $P_c = 1.0$; that is, the range that requires no correction for extrusion and avoidance. For the standard net, P_c reaches a maximum of 0.86 at 4.25 mm and remains above 0.75 only over the interval 3.75–5.50 mm (Fig. 1). In other words, no interval within the larval length range of nehu (2.5–25.0 mm) is sampled completely with the standard net.

A second way of judging the efficacy of the standard net is by the length range than can be corrected, with sufficient precision, for extrusion and avoidance. The effect of correcting a large sample of nehu length frequencies for extrusion and avoidance can be seen in the frequency distributions before and after N_o was divided by the estimated value of P_c (Fig. 4). The precision of this correction can be gauged from the estimates of the variance of N (Fig. 5). Note that variance increases gradually with length until 6.75 mm and, thereafter, increases at a greatly accelerated rate. If 6.75 mm is chosen as the upper bound on the length interval within which the estimated numbers are considered sufficiently precise, then only one-third of the larval length range could be corrected to reflect the true length distribution. Thus, judging from either perspective, the standard net is a relatively ineffective tool for sampling nehu larvae.

Variance of the corrected length-frequency distribution was used above to define some length range that can be corrected for extrusion and avoidance with sufficient precision, but estimates of variance have other important uses,

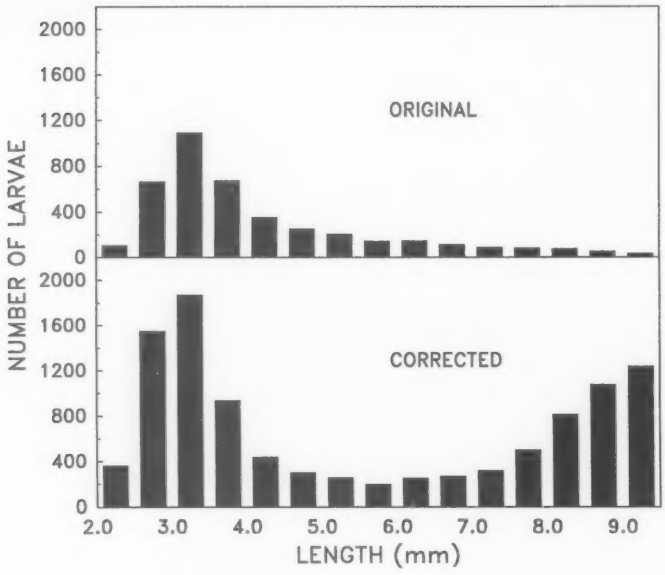

FIGURE 4.—Length distribution of nehu larvae by 0.5 mm intervals before correction for extrusion and avoidance (upper panel) and after correction (lower panel).

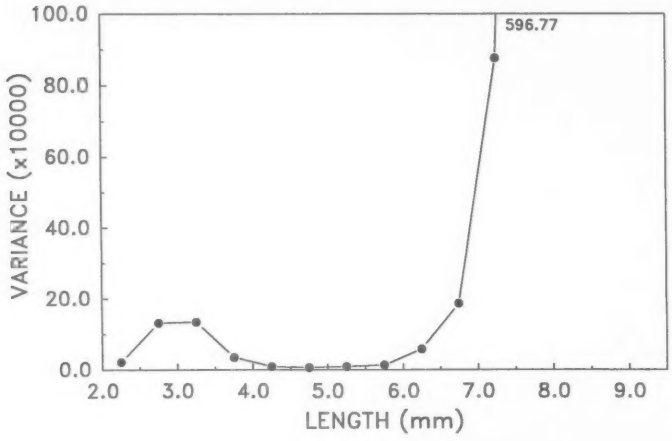

FIGURE 5.—Bootstrap estimate of variance of the corrected number of larvae by 0.5 mm length intervals.

especially when the corrected length-frequency distributions will be subsequently used to estimate mortality rates. Whether mortality is estimated by using methods that require converting length-frequency distributions to age-frequency distributions (Leak and Houde 1987) or by using some form of length-based method (Wetherall et al. 1987), precision of the mortality estimates will depend on the precision of corrected length-frequency distributions. Thus, procedures used to estimate mortality from larval length-frequency distributions should include weighting factors that incorporate the size-specific variances of the corrected length-frequency distributions.

Most of the problems associated with violations in the assumptions $P_{rs} = P_{re}$ and $P_{es} = P_{er}$ could be eliminated with proper attention to the

design of the entry and retention experiments. When these assumptions are violated, unbiased estimates of entry and retention probabilities can sometimes be obtained by restricting the analysis to either large or small larvae to ensure that avoidance and extrusion do not simultaneously influence the size distribution. If the size range of interest must be as broad as possible, however, then the methods described in this paper can be used to correct for differential extrusion and avoidance and unbiased length-frequency distributions can thereby be obtained.

ACKNOWLEDGMENTS

We thank Kevin Landgraf for helping with the field sampling and Tina Xavier for measuring the larvae. George Boehlert, Tom Clarke, Nancy Lo, Bruce Mundy, Jeffrey Polovina, and two anonymous referees reviewed the manuscript and offered helpful suggestions.

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Midgut Cell Height Defines Nutritional Status of Laboratory Raised Larval Northern Anchovy, *Engraulis mordax*

Gail H. Theilacker and Yoshiro Watanabe

ABSTRACT: The height of the midgut mucosal cells was developed as a diagnostic index to assess the past feeding history of larval northern anchovy and to estimate starvation mortality of larval fishes in the sea. The index was compared to traditional histological indices and tested for field use. The height of the mucosal cells was a sensitive index, yielding reliable estimates of larval condition. Because it was sensitive, easy to measure and dependable in formalin-fixed tissue, this diagnostic index should be useful and practical for field work. Additionally, unlike other diagnostic criteria, it resisted the effects of autolysis (withstood prolonged time in the collecting net). Also included is a discussion of the growth characteristics of northern anchovy larvae that experienced a delay in feeding.

Larval mortality may determine recruitment of young fish to a fish stock. A major cause of larval mortality is starvation (Hunter 1976a; Lasker 1981). Several techniques have been recently developed to estimate the proportion of natural mortality caused by starvation. A histopathological technique that uses cellular criteria to identify larval nutritional condition was calibrated in the laboratory (O'Connell 1976; Theilacker 1978; Martin and Malloy 1980), applied to field studies to yield assessments of larval nutritional condition (O'Connell 1980; Theilacker 1986; Margulies 1986; Setzler-Hamilton et al. 1987), and successfully used to estimate rates of starvation-induced mortality (Theilacker 1986). Another technique that employs a morphometric approach generated good predictions of nutritional condition for several larval fish species (Theilacker 1978, 1986; Martin and Malloy 1980; Martin and Wright 1987; Setzler-Hamilton et al. 1987) as did the use of an RNA/DNA index (Buckley 1979; Wright and Martin 1985; Clemmesen 1987; Buckley and Lough 1987; Setzler-Hamilton et al. 1987).

Each of these diagnostic techniques suffers from various constraints. To develop histological criteria, an accurate representation of the structure of live tissue is needed for identifying larval fish condition. The usefulness of these criteria depends on the tissue quality of the field-collected specimens. For many fishes (northern anchovy and striped bass, *Morone saxatilis* (O'Connell 1980; Setzler-Hamilton et al. 1987)), autolytic tissue decomposition occurs within 2–3 minutes after sampling. Because routine ichthyoplankton collections usually take 21 minutes (Smith and Richardson 1977), special plankton collections are required for histopathology. Additionally the routine solution (3–5% formalin) used to preserve plankton does not adequately preserve cellular structure of larval fishes and special solutions (Bouin's fixative) must be used (O'Connell 1976; Theilacker 1978). The morphometric analysis requires extensive calibration studies to estimate the effect of the net and preservatives on shrinkage of body parts because the morphometric indices are very sensitive to shrinkage (Theilacker 1980; 1986). The RNA/DNA index must be calibrated for temperature effects and animal age (Ota and Landry 1984; Buckley 1984; Buckley and Lough 1987); however, there are other considerations that may limit its application. Furthermore, RNA/DNA is generally regarded as an index of potential growth (protein synthesis rates) not starvation mortality.

In March of 1985, we anticipated applying the histopathological technique developed by O'Connell (1976) to estimate starvation rates of northern anchovy collected at two sites off the coast of California (see Owen et al., 1989). However, when aboard ship, we found that it was impossible to preserve the larvae within the required 2–3 min time period (needed to maintain tissue quality) and take a sample that was representative of the zone inhabited by larval anchovy. We were unable to use the established histological criteria because it took us 5 or more minutes to sample larval anchovy from 50 m to the surface and process our collection. Thus, to estimate anchovy starvation rates, we needed to develop

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new criteria that were stable for a longer period.

Here we describe and evaluate a diagnostic index, the height of midgut mucosal cells of larval northern anchovy. The index is sensitive to feeding history, resistant to autolysis (withstands prolonged time in a collecting net), and simple to measure. It is reliable for fish fixed in formalin, the commonly used fixative for field collections.

METHODS

Experimental Design

We raised larval northern anchovy under different feeding conditions to produce specimens that exhibited various health states. These larvae were used to describe growth, determine the dominant midgut height measurement within each feeding treatment, evaluate the midgut index, and estimate response times. In a second series of experiments, groups of fed and starved fish were treated with nets in a manner designed to simulate plankton collection methods in the sea. These studies were used to evaluate how useful the new criterion would be in a field situation.

Rearing Treatments

Five groups of anchovy were raised at 15.5°C for three weeks in 100 L containers. The eggs, stocked at 10/L, were collected from a hormone-injected broodstock maintained at the Southwest Fisheries Center aquarium (Leong 1971). We fed the control group ad libitum on *Gymnodinium* and *Brachionus* (Lasker et al. 1970; Theilacker and McMaster 1971) at yolk absorption (four days after hatching at 15.5°C; hatching = day 0), and delayed feeding 1–4 days in the other groups. Fish were sampled daily from the fed, starved, and delay-fed treatments and preserved in Bouin's fixative (Table 1).

Field Simulation Experiments

One group of northern anchovy was fed for 3 days and one was starved for 3 days. We treated samples from each group of 7 d old fish in a net by flushing the submerged net with 15.5°C seawater for 0, 2, 5, 10, 15, 20, and 25 minutes (see Theilacker 1980 for details of this method). After the net treatment, fish were preserved in either 5% buffered formalin (standard shipboard fixative) or Bouin's solution (required fixative for histopathology).

Histological Preparation

We measured the standard length (SL) of preserved larvae to the nearest 0.01 mm and subsequently prepared them for histopathology using standard microtechniques (O'Connell 1976). Tissue was dehydrated, embedded in paraffin, serially sectioned at 6 μm in the sagittal plane, mounted, and stained with hematoxylin and eosin.

Measurement of Midgut Cell Height

The midgut is the major part of the intestine of

TABLE 1.—Standard length (SL) and

	Fed					
	Growth			Midgut		
Age (days)	*n*	SL[1] $\bar{x}$ mm	SD	*n*	SL[1] $\bar{x}$ mm	mght[2] $\bar{x}$ μm
4	FED					
5	32	3.95	0.23	10	3.93	19.63
6	34	3.92	0.21	17	3.87	20.13
7	26	4.33	0.24	13	4.29	19.52
8	33	4.59	0.46	19	4.67	19.13
9	33	5.29	0.40	10	5.26	22.13
10	38	5.54	0.33	10	5.85	21.88
11	26	6.22	0.47	10	6.09	21.13
12	55	6.36	0.48	10	6.52	20.75
13	38	6.85	0.43			
14	36	7.20	0.54			
17	66	7.22	0.74			
19	35	7.43	0.80			
Total *n*	452			99		

	Starved 3 d/fed					
	Growth			Midgut		
Age (days)	*n*	SL[1] $\bar{x}$ mm	mght[2] $\bar{x}$ SD	*n*	SL[1] $\bar{x}$ mm	mght[2] $\bar{x}$ μm
4	STARVED					
5	STARVED					
6	STARVED					
7	28	3.37	0.22	13	3.29	10.19
8	25	3.35	0.15	13	3.35	9.90
9	29	3.79	0.24	10	3.83	11.38
10	26	3.90	0.25	17	3.93	12.28
11	36	3.92	0.19	11	3.96	14.21
12	34	4.00	0.35	10	4.00	14.88
13	31	4.25	0.38			
14	26	4.63	0.41			
17	31	5.27	0.45			
19	30	5.51	0.68			
24	34	6.80	0.90			
Total *n*	330			74		

[1] SL taken on Bouin's fixed larvae
[2] Midgut cell height (see text)

larval northern anchovy; it extends from behind a constriction at the pylorus to another constriction at the beginning of the hindgut (Fig. 1). We measured the cell heights under a light microscope using the histological preparations. Epithelial cells of the midgut tend to decrease in height from the anterior part to the posterior end. We chose the midpart of the midgut (from 2/5 to 3/5 of the entire length) as the measurement site. The area is easily located in histological sections that are cut parallel to the median plane. The dorsal and ventral rows of midgut cells appeared in these sections. We measured the cells of the ventral row that were larger than the dorsal row, probably because of greater absorptive activity. We selected a section having four to six neighboring cells in which the nuclei, brush border, and cell base were clearly defined; brush border may be indistinct in larvae of poor condition. Measurements were taken from the luminal surface of the brush border to the cell base delimited by a basement membrane, using a micrometer attached to an eye lens. Usually, in sagittal sections, the cell heights are not so varied within the middle part of the midgut. If, however, there were slight differences between cells due to a slight angle of the section, we took an average of several measurements.

midgut cell height (mght) statistics for fed northern anchovy by diet and age.

	Starved 1 d/fed						Starved 2 d/fed					
	Growth			Midgut			Growth			Midgut		
Age (days)	*n*	SL^1 $\bar{x}$ mm	SD	*n*	SL^1 $\bar{x}$ mm	$mght^2$ $\bar{x}$ µm	*n*	SL^1 $\bar{x}$ mm	SD	*n*	SL^1 $\bar{x}$ mm	$mght^2$ $\bar{x}$ µm
4	STARVED						STARVED					
5	33	3.55	0.20	12	3.95	14.27	STARVED					
6	47	3.59	0.37	15	3.60	15.83	27	3.58	0.22	18	3.57	13.47
7	61	3.46	0.23	11	3.45	14.89	33	3.39	0.18	10	3.35	11.88
8	23	3.81	0.31	10	3.77	16.00	31	3.58	0.21	17	3.60	12.21
9	49	4.34	0.46	11	4.79	19.32	18	4.07	0.21	10	4.02	14.63
10	46	4.90	0.39	10	4.80	18.63	38	4.25	0.32	11	4.19	14.77
11	55	5.09	0.56				41	4.58	0.31	10	4.60	15.63
12	71	5.56	0.47				28	4.95	0.39			
13	47	5.86	0.45				27	4.99	0.41			
14	61	6.32	0.62				46	5.63	0.45			
17	121	6.84	0.86				33	6.25	0.73			
19	26	7.19	0.95				39	6.65	0.93			
Total *n*	640			69			361			76		

	Starved 4 d/fed					
	Growth			Midgut		
Age (days)	*n*	SL^1 $\bar{x}$ mm	SD	*n*	SL^1 $\bar{x}$ mm	$mght^2$ $\bar{x}$ µm
4	STARVED					
5	STARVED					
6	STARVED					
7	STARVED					
8	19	3.40	0.19	10	3.44	10.51
9	14	3.58	0.22	6	3.59	10.00
10	6	3.66	0.12	6	3.66	8.13
11						
12						
13						
14						
17						
19						
24						
Total *n*	39			22		

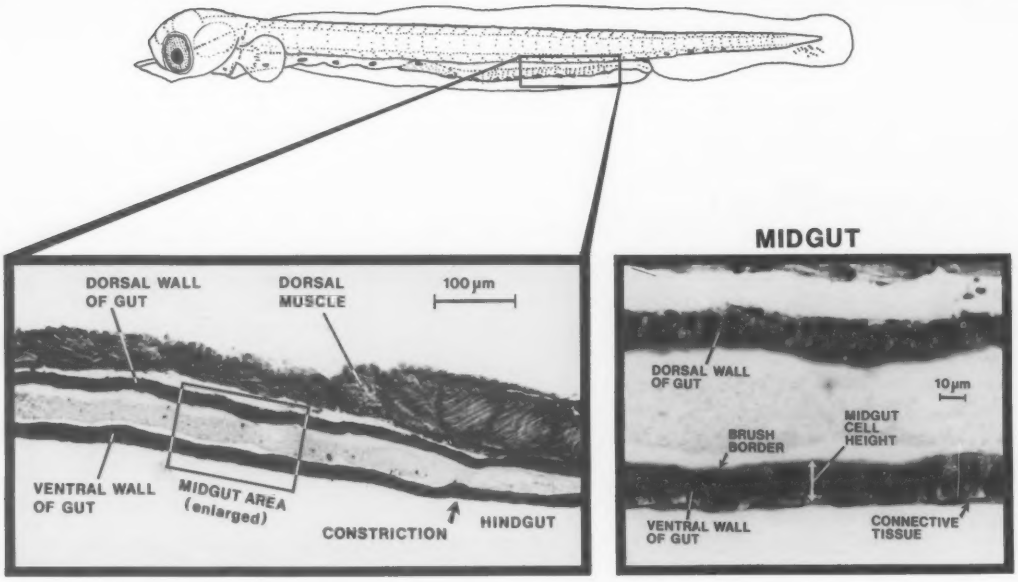

FIGURE 1.—*Engraulis mordax* larva showing measurement site for midgut cell height.

Evaluation of Midgut Criteria

To evaluate the capacity of the midgut cell height measurement to classify larval anchovy condition, we graded 5–10 larvae taken daily from 3 treatments (fed, feeding delayed 1 day, and starved) using both O'Connell's (1976) histological criteria and the midgut cell height. We assumed that the histological criteria (the sum of the cellular grades for the brain, cartilage, notochord, musculature, liver, and midgut) would yield the best estimate of larval condition, and we compared the power of each index to predict past feeding history.

RESULTS

Diet-Induced Differences in Growth

Growth of the fed control group was 0.41 mm/d, similar to published reports for northern anchovy raised in the laboratory (Kramer and Zweifel 1970; Hunter 1976b; Theilacker 1987). Larvae experiencing a feeding delay of 1, 2, and 3 days were smaller at 10.8 days than larvae not experiencing a delay, and as the starvation interval increased, their final size decreased (Table 2). For the test of significance of size at age, P was <0.01 for all delay combinations except the starved 3 d/fed (S3/F) vs. the 4 d delay in feeding

TABLE 2.—Diet-induced differences in growth of northern anchovy at a common age and at a common feeding period (n's for common feeding period slightly less than n's for common age).

	Common age				Common feeding period		
Diet	n	Age d	Feeding period d	SL $\bar{x}$ mm	Age d	Feeding period d	SL $\bar{x}$ mm
Fed	452	10.8	6.8	5.58	10	6	5.51
Starved							
1 d/fed	640	10.8	5.8	4.87	11	6	4.96
2 d/fed	394	10.8	4.8	4.48	12	6	4.75
3 d/fed	372	10.8	3.8	4.00	13	6	4.32
4 d/fed	114	10.8	2.8	3.98	—	—	—

(S4/F) where $P = 0.8$, indicating that delaying feeding affected the final fish size at a given age (ANOVA; Table 2).

Progressively increasing the periods of starvation before feeding also caused a decrement in the growth rate after feeding resumed (Fig. 2; Table 2). Larvae were unable to compensate for a delay in feeding at the onset, and fish length at an age where all fish had been feeding for 6 days differed for each treatment [$P = < 0.01$ for all diet combinations except starved 1 d/fed (S1/F) vs. 2 d delay in feeding (S2/F) where $P = 0.08$ (ANOVA; Table 2)]. Growth rates for the 6 d period ranged from 0.41 mm/d for the fed group, 0.39 mm/d for 1 d delay in feeding (S1/F), 0.34 mm/d for 2 d delay (S2/F), 0.31 mm/d for 3 d delay (S3/F). Length was transformed to natural logs for the ANOVAs. The test for the equality of slopes showed that all slopes differed ($P = <0.0001$ for all combinations). Thus, delaying feeding affected the final fish size and caused a decrement in the growth rate after feeding resumed.

Evaluation of Midgut Cell Height Criterion

For a subset of northern anchovy larvae taken from the treatments where larvae were fed, starved, and feeding was delayed 1 day (S1/F), we compared the number of larvae correctly classified to feeding treatment by the midgut cell height and by the traditional histological index (O'Connell 1976). To define the midgut cell height interval for each feeding treatment, we selected the midpoint between successive cell height means (Table 3) as the interval breakpoint for predicting feeding history from cell height. The midgut cell height was correlated with the histological score (Fig. 3, $n = 38$, $P < 0.001$, t-ratio = 25.85). Both the cell height and the histological score correctly classified all of the subset larvae that were fed to the correct group and 78 and 79% of the starved larvae to the correct group. On the other hand, for the delayed feeding group (S1/F), the midgut cell height was a better predictor of feeding history than the histological score. The midgut measurement classified 78% correctly whereas the histological score classified only 50% correctly.

After the apparent success of this evaluation, we used the midgut cell height data set (Table 1; Fig. 4) to establish the criteria needed to define and calibrate the midgut cell height measurement for predicting feeding history and for calculating starvation rates of anchovy larvae in the sea.

Diet and Midgut Cell Height Categories for Larvae <4.0 mm

We defined the diet and cell height categories for first-feeding larvae (<4.00 mm SL) which are vulnerable to starvation. The height of the

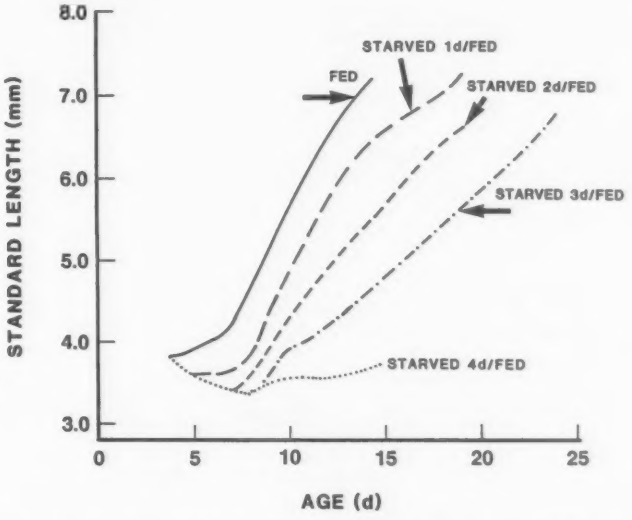

FIGURE 2.—Growth of *Engraulis mordax* larvae under different feeding conditions.

TABLE 3.—Midgut cell height (mght) statistics for six diets by northern anchovy size.

Size Interval (mm)	Fed *n* $\bar{x}$ mght (μm) SD	Starved 1 d/fed *n* $\bar{x}$ mght (μm) SD	Starved 2 d/fed *n* $\bar{x}$ mght (μm) SD	Starved 3 d/fed *n* $\bar{x}$ mght (μm) SD	Starved 1 & 2 d *n* $\bar{x}$ mght (μm) SD	Starved 3 & 4 d *n* $\bar{x}$ mght (μm) SD	All
<4.00	20 20.50 2.27	31 15.56 3.18	33 12.58 2.12	41 11.77 2.44	28 13.48 2.81	24 10.38 2.00	176
4.00–4.99	40 19.47 3.67	18 17.36 3.58	27 15.28 2.51	20 13.68 2.64			105
5.00–5.99	21 20.95 2.71	8 20.63 3.78					29

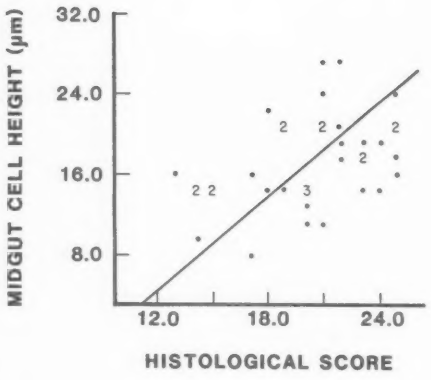

FIGURE 3.—*Engraulis mordax* larvae, regression of midgut cell height measurement on histological score.

midgut cells decreased from the fed to the starved state. The average height of the midgut cells in fed fish <4.00 mm was 20.5 μm. The height averaged 15.6 μm when feeding was delayed one day, 12.6 μm for a 2 d delay and 11.8 μm for a 3 d delay in feeding. The mean midgut height for larvae starved 1 and 2 days was 13.5 μm and for the 3 and 4 d starved group was 10.4 μm (Table 3; Fig. 5).

The height of midgut cells of the fed group (fed) and those where feeding was delayed 1 day (S1/F) was different from all other groups (ANOVA P's < 0.01; Table 4). Fish starved 3 and 4 days (S3&4) also differed from all others (P's < 0.05 level). On the other hand, midgut cell heights of larvae starved 1 and 2 days (S1&2) were not different from those of larvae in which feeding was delayed 2 or 3 days (S2/F and S3/F) (P's = 0.16 and 0.17; Table 4). The t-test matrix indicated four distinct diet and cell height

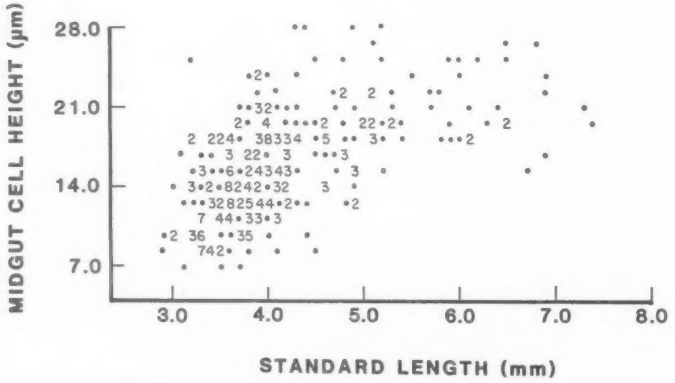

FIGURE 4.—Midgut cell height measurements for *Engraulis mordax* larvae that were raised in the laboratory. Fish were either fed, starved, or feeding was delayed.

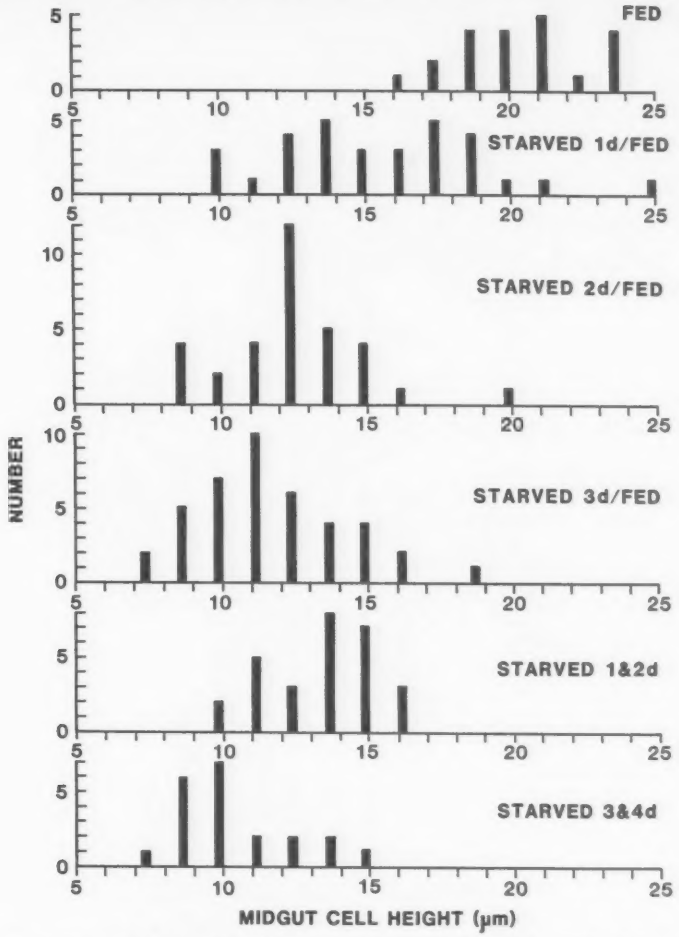

FIGURE 5.—Midgut cell height measurements for *Engraulis mordax* larvae <4.00 mm raised using various feeding conditions.

TABLE 4.—Paired comparison of midgut cell heights for six diets for northern anchovy <4.00 mm SL: *t*-test matrix and probabilities ($P = < 0.01$, **; $P = < 0.05$,*; $P = > 0.05$, value).

		Starved				
	Fed	1 d/fed	2 d/fed	3 d/fed	1 & 2 days	3 & 4 days
Fed	0.0000					
Starved						
1 d/fed	− 6.8438**	0.0000				
2 d/fed	−11.1211**	−4.7522**	0.0000			
3 d/fed	−12.7320**	−6.3433**	−1.3731/.17	0.0000		
1 & 2 days	− 9.5331**	−3.1765**	1.4029/.16	2.7802**	0.0000	
3 & 4 days	−13.1632**	−7.4916**	−3.2143**	−2.1187*	−4.3834**	0.0000

categories for first-feeding larvae: 1) a fed category, 2) a category for 1 d delay in feeding (S1/F), 3) an intermediate category (S2/F + S3/F + S1&2), and 4) a starved category (S3&4).

Calibrations for Field Studies

To estimate daily starvation rates in the sea using cell height, an approximation of the dura-

tion or response time for each size, diet, and cell height category is needed. The duration is the number of days that larvae belonging to the size, diet, and cell height category remain within that category. Daily rates in the sea (estimates of numbers of larvae per day) are determined by dividing the number of field-collected larvae classified to each category by the category duration. See the following section on "Applying the Calibration Criteria" for a more detailed explanation of this procedure.

Duration for Fed Category, <4.00 mm SL

Fed larvae began to eat at 3.8 mm (preserved length), yet there was little or no growth for 2 days (Fig. 2). Even though, on the average, the fed anchovy grew at 0.41 mm/d, when the delay in growth was considered, the resulting duration for the <4.00 mm fed group was 2.5 days. Thus it took 2.5 days for the fed fish to move out of this size, diet, and cell height category. This initial lag in growth was reported earlier for northern anchovy (Theilacker 1987).

Durations for Intermediate Categories, <4.00 mm SL

The durations were 5 days for diet groups where feeding was delayed 1 and 2 days (S1/F and S2/F). The group that was starved 3 days before feeding (S3/F) remained within the midgut cell height interval for 8 days (Table 1). The duration for larvae that were starved for 1 and 2 days (S1&2) was 2 days.

Duration for Starved Category, <4.00 mm SL

The duration for the group starved 3 and 4 days (S3&4) was 2 days. Northern anchovy larvae died after starving 3–4 days. No larvae belonging to the starved category were larger than 4.0 mm.

Field Feasibility Study

Because larval fish tissues decompose rapidly due to autolysis (Theilacker 1978; O'Connell 1980), we tested the effects that the prolonged processing periods encountered at sea have on the integrity of the midgut cells. In this study, after 5 minutes in the net, the condition of both formalin- and Bouin's-fixed larval tissues could not be graded using traditional histological criteria due to indistinct nucleoli, diffused nuclei, and intercellular spaces. However, measurement of midgut cell height was still possible after 25 minutes.

The height of the midgut cells, whether measured in formalin- or Bouin's-fixed individuals, showed little change in height over the 25 min processing period (Fig. 6a–d; slope b is not significant from 0; $P = 0.494$ and 0.596 for the formalin group and 0.077 and 0.039 for the Bouin's group, Table 5). Although the height of midgut cells is stable within each diet and 1 mm interval size category (Table 3), we weighted the midgut cell height by fish size for this analysis because it included both fed and starved larvae ranging between 2.8 and 5.6 mm. When the midgut height of fish belonging to all diets was plotted over the 2.8–5.6 mm size range, midgut cell height increased linearly with size (Fig. 4). And, because the fish shrink in the collecting net and the amount of shrinkage is related to the time elapsed in the net, we adjusted fish lengths in this analysis to equal "capture" size using the model developed by Theilacker (1980).

Applying the Calibration Criteria

In practice, when applying this analysis to the field to estimate starvation-induced mortality rates (Owen et al. 1989), it was deemed necessary to use only three diet categories (fed, intermediate, and starved) instead of the four distinct categories determined by ANOVA (Table 4), and discussed earlier. Because the durations were 5 days for both diets where feeding was delayed 1 and 2 days (S1/F and S2/F), there was no need for the S1/F larvae to be a separate, fourth category. Thus we included S1/F in the intermediate category and selected 5 days as an average duration for the <4.00 mm larvae in this category.

The cell-height intervals for the three categories were the midpoints between the means of the group cell heights determined for the laboratory-reared larvae. We regarded all larvae with a midgut height measurement >17.5 μm as belonging to the fed category; the break between the intermediate and starving categories was 11.25 μm. This classification scheme correctly identified 95% of the fed larvae, 77% of the starved larvae, and 74% of the intermediate larvae <4.00 mm SL.

To calculate the starvation rates of northern anchovy larvae in the sea, we measured the length of each field-collected larva (corrected for

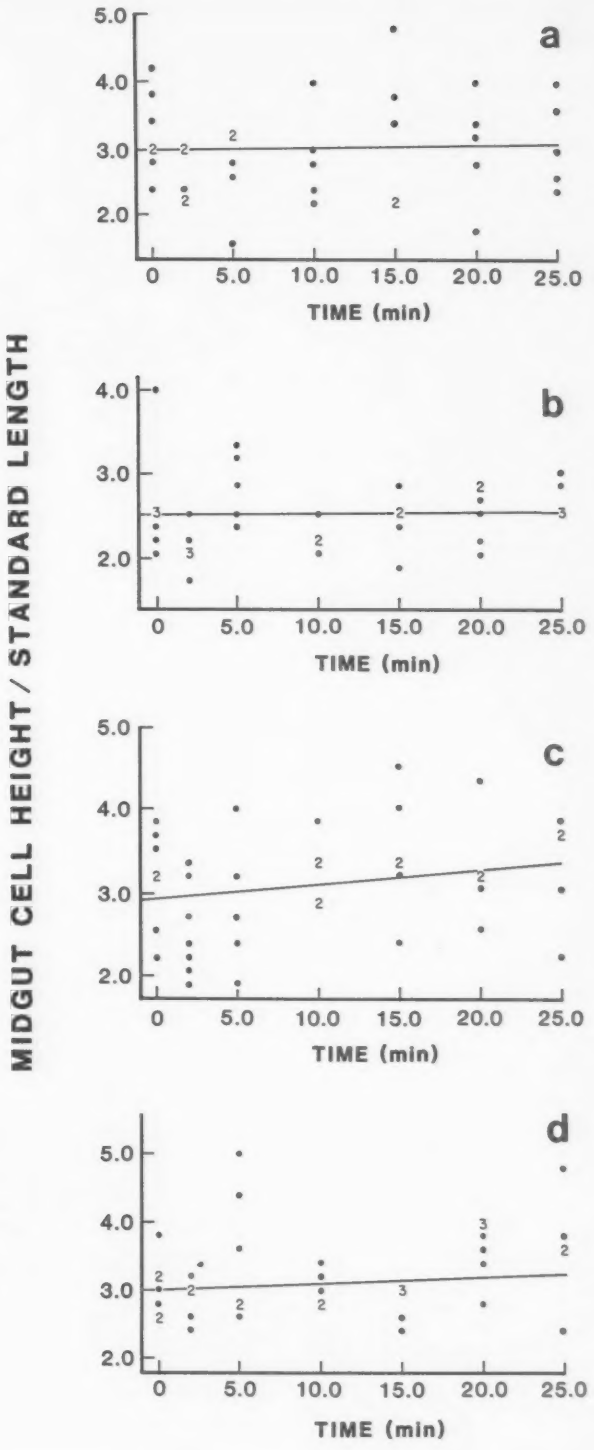

FIGURE 6.—a) Change in midgut cell height measurement over time for formalin-fixed *Engraulis mordax* larvae that were fed. b) Change in midgut cell height measurement over time for formalin-fixed *Engraulis mordax* larvae that were starved. c) Change in midgut cell height measurement over time for Bouin's-fixed *Engraulis mordax* larvae that were fed. d) Change in midgut cell height measurement over time for Bouin's-fixed *Engraulis mordax* larvae that were starved.

shrinkage due to time-in-net and preservation (Theilacker 1980)) and the height of the midgut cells. The adjusted SL and absolute midgut cell height classifies each larva into a size, diet, and midgut cell height category. The numbers of larvae belonging to each category are divided by the category durations to yield the number of larvae per day per category. To estimate the percentage of larvae dying per day due to starvation, the starved category is divided by the total number. An example of these manipulations in Table 5 (taken from Owen 1989; this issue) shows that mortality due to starvation was estimated to be 24%/d for first-feeding anchovy larvae collected off southern California.

TABLE 5.—Histological condition of larval northern anchovy off southern California. (From Owen et al. 1989: table 7.)

		INSHORE SITE I				
		Categories				
SL mm		Fed "healthy"	Interme-diate	Starved	Total	%/d
<4.00	Number[1]	28	17	9		
	Duration[2]	2.5	5	2		
	No./d[3]	11.2	3.4	4.5	19.1	24

[1]Number of field-collected larvae belonging to each size, diet, and midgut-cell-height category.
[2]Response times for each size, diet, and midgut-cell-height category (see text).
[3]Number/duration = No./d.

To complete these manipulations for the next size class, 4–<5 mm, fed and intermediate larvae were discriminated using the same cell height measurement, 17.5 μm, and starved larvae did not grow into this size class (Table 3). The duration for the fed category was 2.5 days and for the intermediate category averaged 3 days. The 2.5 d duration for the fed category was obtained by dividing the size-class interval by the growth rate, 0.41 mm/d. Larvae from the delayed-feeding treatments that belonged to the intermediate category outgrew this size class within 2–4 days (Table 1). Some larvae belonging to the group where feeding was delayed 1 day (S1/F) had recovered and entered the fed category by the time they grew to 4.00 mm.

Cell heights cannot be measured for northern anchovy larger than 6 mm SL as the midgut folds, increasing the absorptive area and making cell heights difficult to measure.

DISCUSSION

The height of northern anchovy midgut cells (taken on sagittal sections that were prepared for histological examination) defines past feeding history. Kostomarova (1962) also measured the height of intestinal cells of larval fishes to evaluate their state of health. Although she found a relation between fish condition and size of midgut cells, the relation was not quantified. In our study, we establish criteria for discriminating the condition of laboratory-raised larvae using the midgut cell height and for estimating rates of starvation in the field.

To validate this technique, it was necessary to measure the effects on the midgut cells of the prolonged processing periods, commonly encountered at sea. The elapsed time for standard ichthyoplankton net hauls to 225 m is 21 minutes, and additional time is needed for washing down the net and for sample preservation (Smith and Richardson 1977). To quantify the effect of collecting time and processing time on autolysis, we simulated the net collection and used a matrix of 8 time periods, ranging from 0 to 25 minutes, followed by preservation in either of two fixatives, Bouin's or formalin. Initially, alcohol also was tested because we anticipated using the same fish to study both growth and condition. (80% alcohol is routinely used to preserve otoliths.) Unfortunately, we found alcohol useless for histopathology.

The height of the midgut cells did not change over the 25 m net treatment, but the standard length decreased. Thus, for field collections, it is not necessary to adjust midgut height for time-in-net, but it is important to correct standard length of field-collected larvae for shrinkage in order to allocate the larvae into the correct length categories. The model (Theilacker 1980) used to adjust length was generated for formalin-preserved anchovy. Perhaps the slight

increase noted in the midgut index (midgut cell height/SL) of the Bouin's-fixed specimens (Fig. 6c, d) indicates that the model is overcorrecting for Bouin's. That is, the additional shrinkage caused by fixation (shrinkage in addition to that due to abrasion by the collecting net) is less when Bouin's is used for the final fixative than when formalin is used. This logic, however, is hard to reconcile because Bouin's, made with 20% formalin, is stronger than the 5% formalin solution we used.

Starved fish may be shrinking more during the net treatment than their fed counterparts, further complicating the interpretation of the shrinkage adjustment. But we cannot be certain that this occurred because we did not follow individual larvae during the net treatment. Yet there was a significant decrease in length of starved larvae when the adjusted lengths (corrected to "live length") were regressed and plotted over time (Fig. 7b; Table 6). The decrease in length was not evident for the fed larvae (Fig. 7a). This apparent difference in shrinkage rates between fed and starved larvae needs to be tested.

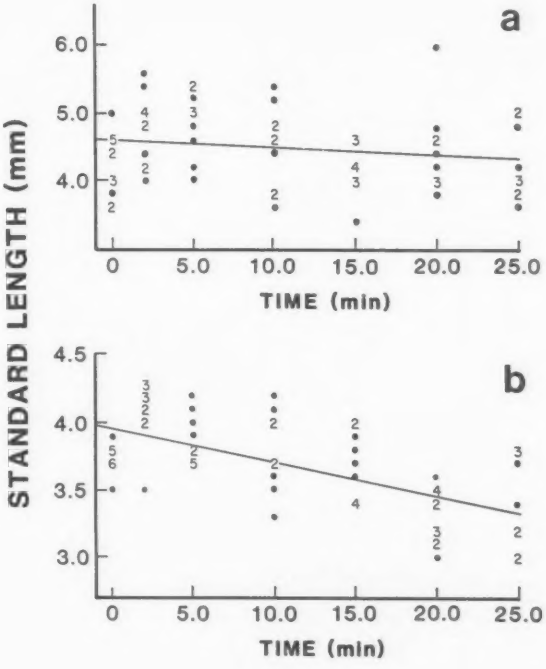

FIGURE 7.—a) Change in standard length over time for fed *Engraulis mordax* larvae that were fixed in formalin and Bouin's. b) Change in standard length over time for starved *Engraulis mordax* larvae that were fixed in formalin and Bouin's.

TABLE 6.—Coefficients for regressions of midgut indexes (midgut cell height/adjusted standard length (mght/SL)) and of adjusted standard length (SL) with elapsed time-in-net (t).

Diet	Measurement	Fixative	Mght/SL = a + bt			Reference figure
			a	b	P	
Fed	Mght/SL	5% formalin	2.8941	0.0092	0.494	6a
Starved	Mght/SL	5% formalin	2.4869	0.0041	0.596	6b
Fed	Mght/SL	Bouin's	2.8961	0.0212	0.077	6c
Starved	Mght/SL	Bouin's	2.9839	0.0231	0.039	6d
Fed	SL	Formalin & Bouin's	3.9605	−0.0251	0.000	7a
Starved	SL	Formalin & Bouin's	4.5813	−0.0124	0.079	7b

Incidental information from delayed feeding experiments (Table 1) revealed that, depending on diet, age of 5 mm northern anchovy ranged between 9 and 19 days. This 10 d range in age at size (due to feeding history) has important implications for size-at-age mortality estimates.

In conclusion, our study indicates that the absolute midgut cell height of northern anchovy larvae is a practical criterion to use for estimating rates of starvation. The cell height measurement yields reliable estimates of feeding history, is resistant to autolysis, and is reliable in formalin-fixed specimens. Thus, the special ichthyoplankton tows and preservatives required for a histopathological index are not needed when the midgut index is used. The midgut index is as sensitive to nutritional conditions as the histological index and does not require the rigorous calibration needed for the morphometric technique (Theilacker 1986; Setzler-Hamilton et al. 1987). Also the midgut character is much easier and faster to measure than scoring the histological features of northern anchovy tissues, and it does not require a solid background in histology for the person scoring. Because of these features, the midgut index is practical for routine estimates of starvation rates of larvae in the sea. In addition, unlike previous methods, the duration of tow is not a constraint because the character does not degrade with time and a sample representative of the water column can be taken.

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Comparative Growth, Mortality, and Energetics of Marine Fish Larvae: Temperature and Implied Latitudinal Effects

Edward D. Houde

ABSTRACT: Vital rates and energetics of marine fish larvae were examined in relation to temperature to determine if recruitment potential and spawning strategies might vary as a consequence of differences in these traits among species. Literature-derived values of growth rates, mortality rates, larval stage durations, gross growth efficiencies, and oxygen uptakes were considered. Results were presumed to reflect latitudinal variation among species. Instantaneous daily growth and mortality rates each increased approximately 0.01 per °C increase in temperature. But, there was no significant regression of gross growth efficiency on temperature (mean K_1 = 0.29), indicating no latitudinal relationship. The large increases in growth rate at high temperatures must be supported by increased food consumption, not increased growth efficiency. Oxygen uptakes also increased significantly in relation to temperature, but relatively slowly compared to growth rates. Larval stage duration was inversely related to growth rate. The potential variability in growth rate was observed to increase with temperature, but the opposite trend was observed for stage duration. Thus, stage durations tended to be both long and potentially variable in high latitudes. Because of these characteristics it is suggested that early life, density-dependent regulation is more probable in high than in low latitudes. The required ingestion to support average growth rate increased threefold in the 10°–30°C range, indicating that fish larvae in warm seas may be more likely to starve than larvae in cold seas. Spawning in low latitudes often is protracted with frequent batches in contrast to spawning in high latitudes, where seasons are brief, with one or a few batches. The different strategies may have been selected and maintained to counter energetic and dynamic constraints in the larval stage.

Variability in growth and mortality rates of marine fish larvae can cause fluctuations in recruitment levels. The two processes, growth and death, may interact and can be viewed as a "single process" in early life (Cushing 1975). In reviewing larval mortality rates, it is apparent that not only are rates high but they range widely (Dahlberg 1979; McGurk 1986). Growth rates also are variable, both among and within species, which could cause significant fluctuations in recruitment levels through effects on larval stage duration (Houde 1987). If variation in the magnitude of larval growth or mortality were predictable, for example, in relation to latitude, the consequences of it might be discernible in life history strategies or in physiological adaptations of fishes from different temperature zones.

Objectives of this paper are to compare vital rates and energetics parameters of marine fish larvae, and to discuss results in the context of spawning strategies and possible mechanisms in the larval stage that may regulate the recruitment process. A cursory examination of literature indicated that teleost larval growth and mortality rates increased relative to temperature and that temperature could, in a general way, be equated to latitude. A review and comparative analysis were undertaken to define the relationships between temperature and the larvae 1) growth rates, 2) stage duration, 3) mortality rates, 4) growth efficiency, and 5) oxygen uptakes. From the analysis, it was possible to estimate cohort net survivorships, to develop energy budgets, and to estimate ingestion requirements of first-feeding larvae over the range of temperatures that was surveyed. The likelihood of starvation by marine fish larvae from low and high latitudes was considered. Because spawning strategies of marine fishes may be linked to larval dynamics and energetics, results also were considered in relation to dominant spawning patterns in warm and cold seas.

METHODS

Literature was reviewed to obtain data for the analyses. Relationships and variables that were

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analyzed are defined in Table 1. Analyses were confined to feeding-stage larvae of marine fishes and to a few anadromous species. Salmonid fishes, which lack a typical larval stage, were not included.

TABLE 1.—Relationships that were analyzed and abbreviations that are used in text.

T	Temperature, °C
G	Weight-specific growth rate, d^{-1}
D	Stage duration, defined as days from hatching to metamorphosis, d
Z	Instantaneious daily mortality coefficient, d^{-1}
K_1	Gross growth efficiency, G/I
I	Weight-specific ingestion rate, d^{-1}
Q_{O_2}	Weight-specific oxygen uptake, μL O_2/mg/h
N_{met}	Net survivorship; fraction of a cohort expected to survive from hatching to metamorphosis

Growth

Weight-specific growth rates (G) of larvae were obtained from laboratory and field studies. Growth coefficients were taken directly from published work, when available, or calculated from the data. In a few cases, length-weight relationships were used to convert growth-in-length data to growth-in-weight. Weight-specific growth data for larvae of some commonly studied species were unavailable and those species could not be included in analyses. Weight-specific growth rates are

$$G = \frac{(\ln W_t - \ln W_0)}{t}$$

where W_0 and W_t are dry weights of larvae at hatch and at the end of a growth period of t days' duration.

A linear regression was fitted to express the relationship of weight-specific growth rates on temperature. Because both G and T for a species sometimes had a considerable range reported in the literature, the midpoints of reported G and T values were selected arbitrarily as the data for each species in the regression analysis. A Q_{10} was estimated from predicted values of G in the range 5°–30°C.

Stage Duration

Stage duration (D) was defined as days from hatching to metamorphosis. As such, it is inversely proportional to weight-specific growth rate (G) and dependent upon species-specific weight at metamorphosis. Stage duration was calculated from the literature-derived data on G, dry weights at hatch (W_0), and dry weights at metamorphosis (W_m)

$$D = \frac{(\ln W_m - \ln W_0)}{G}.$$

A power regression was fitted, in which the geometric midpoint, i.e., antilog [($\log_{10}$ low D + $\log_{10}$ high D) * ½] of the estimated range of D for each species was regressed on the estimated midpoint of temperature, to describe the relationship between stage duration and temperature.

Mortality

Instantaneous daily mortality coefficients (Z) of post-yolk-sac larvae were obtained from published field studies in which the rates had been determined or could be calculated from the authors' estimated abundances-at-age. Much of the mortality data was obtained from summaries and references in papers by Dahlberg (1979) and McGurk (1986), supplemented with Z estimates from additional and more recent sources.

A linear regression of the midpoints of the estimated range of Z on the midpoints of T for each species was fitted to describe the relationship between $Z$and T.

Relationship Between Mortality and Growth Rates

Solution of the equation for growth rate on temperature in terms of temperature and its substitution into the equation for mortality rates on temperature yielded an expression relating mortality rates to growth rates.

Net Survivorship

Based on the estimates of growth rates, stage duration, and mortality rates predicted from the regressions, the proportion of a cohort expected to survive to metamorphosis (N_{met}) was calculated for 10°, 20°, and 30°C. The percentage cohort survivorship at each of the temperatures was calculated from the exponential relationship

$$100\, N_{met} = e^{-ZD}.$$

Effects on survivorship of decreases in G and

increases in Z also were determined at those three temperatures.

Growth Efficiency

Gross growth efficiency (K_1) is the proportion of ingestion that goes to growth;

$$K_1 = G/I\ ,$$

where G is the weight-specific growth rate and I is the weight-specific ingestion rate. Growth efficiencies and temperatures (T) in published reports were examined. An attempt was made to fit a linear regression to midpoints of K_1 regressed on midpoints of T for species where data were available.

Because $I = G/K_1$ and the regression relationship between G and T had been defined, weight-specific ingestion rate also could be related to temperature. That expression was applied to estimate the weight-specific ingestion rate required to attain mean, among-species growth rates in relation to temperature. It was assumed that an average food particle for a first-feeding larva weighed 0.25 μg dry weight. Then, the number of particles required to attain average growth rate and the consequences of changes in temperature on that requirement were explored. The regression relationship between I and G also was examined to determine the rate of increase in ingestion necessary to support increased growth.

Metabolism

The Q_{O_2}, i.e., weight-specific oxygen uptakes, were obtained for marine fish larvae where data were available. Values were taken directly from literature or derived if the relationship between oxygen uptake and larval dry weight was reported. Values used here were confined to those for feeding or end-of-yolk-sac stage larvae. The midpoints in the range of Q_{O_2} for a species were regressed on the midpoints of the temperature values to obtain a relationship between weight-specific oxygen uptake and temperature. A Q_{10} was derived from the predicted values of Q_{O_2} in the 5°–30°C range.

Energy Budgets

Energy budgets for average first-feeding larvae at 10°, 20°, and 30°C were developed from the information and relationships on growth rates (G), oxygen uptake (Q_{O_2}), and ingestions (I). Budgets were expressed as

$$I = G + M + F$$

where M is metabolism and F is feces. The Q_{O_2} was converted to M using an oxycalorific equivalent of 0.00463 cal/μL O_2 (Brett and Groves 1979). The oxygen uptake estimates reported in the literature generally were made on "resting" or anesthetized larvae. These estimates were presumed to represent routine metabolism. For the energy budgets, the reported Q_{O_2} values were multiplied by 2.0 to estimate active metabolism for 12 hours of the day, the time that a larva was assumed to swim actively while feeding (i.e., daylight hours). The estimated Q_{O_2} from the regression relationship was assumed to apply during the remaining 12 hours. The 2.0 multiplier is commonly used, but may be conservative (Brett and Groves 1979). If metabolism has been underestimated, the absolute values of budget components are in error but relative effects of temperature on the larval energy budgets still will be expressed.

Both ingestion rates and growth rates were converted from dry weight to calories by assuming an equivalency of 5,000 cal/g dry weight. Values for feces in the energy budgets were obtained by difference. Energy budgets were expressed both in absolute and relative (i.e., percent) terms. After the energy budgets had been determined, assimilation efficiencies, $A = (G + M)/I$, and net growth efficiencies, $K_2 = G/(G + M)$, were derived and compared among temperatures (see Table 8).

RESULTS

Growth

Weight-specific growth coefficients ranged from <0.01 to >0.55, indicating a widely varying potential for growth among species of marine fish larvae that was strongly related to temperature and, presumably, latitude (Table 2; Fig. 1). Relative growth-in-weight ranged from <1% to >73% d^{-1}. The regression of midpoint G on midpoint T for 27 species indicated an approximate 0.01 increase in G for each degree increase in T.

$$G = -0.0036 + 0.0094\,T$$

$$r^2 = 0.57 \qquad S_b = 0.0016. \qquad (1)$$

TABLE 2.—Weight-specific growth coefficients (G) from laboratory and field-estimated growth rates of marine fish larvae. Temperatures (T), dry weight ranges, and mid-points of estimated G and T also are given. Values were taken directly from published results, calculated from the authors' data or calculated from available length-weight relationships.

Species	Temperature		Dry weight range (mg)	Growth coefficient (G)		References
	Range	Midpoint		Range	Midpoint	
Clupea harengus CH	06.0–17.0	11.5	0.06–100.00	<0.01–0.12	0.065	McGurk (1984) and numerous references therein; Gamble et al. (1985); Kiorboe and Munk (1986); Kiorboe et al. (1987)
Chanos chanos CC	25.0–29.0	27.0	0.25–60.00 (wet wts)	0.12–0.17	0.145	Liao et al. (1979); Duray and Bagarinao (1984)
Anchoa lamprotaenia ALa	26.0	26.0	0.02–0.06	0.21	0.210	Chitty (1981)
Anchoa mitchilli AM	23.0–31.0	27.0	0.01–6.00	0.15–0.35	0.250	Houde (1977d, 1978); Houde and Schekter (1981); Leak and Houde (1987); Houde (unpub. data)
Engraulis mordax EM	13.0–16.0	14.5	0.02–0.50	0.14–0.30	0.220	Hunter (1976); Methot and Kramer (1979); Smith (1985); Theilacker (1987)
Gadus morhua GM	4.0–11.0	7.5	0.05–3.00	0.02–0.12	0.070	Laurence (1978); Buckley (1979); Laurence et al. (1981); Gamble and Houde (1984); Øiestad (1985); Buckley and Lough (1987)
Melanogrammus aeglefinus MA	4.0–9.0	6.5	0.07–2.90	0.01–0.13	0.070	Laurence (1974, 1978); Laurence et al. (1981); Bergen et al. (1985); Buckley and Lough (1987); Buckley et al. (1987)
Merluccius productus MP	10.5–15.0	13.0	~0.04–~1.80	—	0.060	Bailey (1982)
Theragra chalcogramma TC	5.0–9.5	7.0	0.04–33.50	0.02–0.13	0.075	Hamai et al. (1974); Clarke (1984); Nishimura and Yamada (1984); Walline (1985); Bailey and Stehr (1986); Kendall et al. (1987)
Menidia menidia MM	19.0–21.0	20.0	~0.50–8.90 (wet wts)	~0.13	~0.130	Beck and Poston (1980)
Menidia peninsulae MP	20.0–30.0	25.0	0.03–2.24	0.08–0.25	0.165	McMullen and Middaugh (1985)
Morone americana MAm	13.0–21.0	17.0	0.02–0.09	0.03–0.18	0.105	Margulies (1986)
Morone saxatilis MS	12.0–22.5	17.0	0.15–15.00	0.09–0.19	0.140	Dey (1981); Eldridge et al. (1981); Rogers and Westin (1981); Eldridge et al. (1982); Houde and Lubbers (1986); Chesney (1986)
Dicentrarchus labrax DL	13.0–20.0	16.5	0.09–~2.80	0.07–0.18	0.125	Girin (1975); Girin et al. (1975); Barahona-Fernandes and Girin (1977); Barahona-Fernandes (1978,1979); Gatesoupe and Luquet (1981); Gatesoupe and Robin (1982)

TABLE 2.—*Continued.*

Species	Temperature Range	Temperature Midpoint	Dry weight range (mg)	Growth coefficient (*G*) Range	Growth coefficient (*G*) Midpoint	References
Haemulon flavolineatum HF	~25.0–~30.0	~27.5	0.02–10.00	~0.24–~0.41	~0.325	McFarland et al. (1985); Saksena and Richards (1975)–data on *H.plumieri*, used to approximate *H. flavolineatum*.
Archosargus rhomboidalis AR	23.0–29.0	26.0	0.01–4.20	0.21–0.41	0.310	Houde (1975, 1978); Stepien (1976); Houde and Schekter (1981)
Pagrus major PM	17.0–23.5	20.0	0.05–13.70 (wet wts)	0.06–0.33	0.195	Fushimi and Nakatani (1977); Kitajima et al. (1980); Fukusho et al. (1984); Kuronuma and Fukusho (1984)
Sparus aurata SA	15.0–20.0	17.5	~0.02–~10.00	0.10–0.14	0.120	Divanach (1985); Tandler and Helps (1985)
Cynoscion nebulosus CN	24.0–32.0	28.0	0.02–1.60	0.16–0.57	0.365	Taniguchi (1979, 1981)
Ammodytes americanus AA	0.0–10.0	5.0	0.04–10.00	<0.01–0.12	0.060	Buckley et al. (1984); Smigielski et al. (1984); Monteleone and Peterson (1986); Buckley et al. (1987)
Scomber japonicus SJ	17.0–22.0	19.5	0.03–34.45	0.25–0.43	0.340	Hunter and Kimbrell (1980)
Scomber scombrus SSc	15.0	15.0	0.05–2.23	0.10–0.18	0.140	Buckley et al. (1987)
Paralichthys dentatus PD	18.0	18.0	–	0.07	0.070	Buckley and Dillman (1982)
Scophthalmus maximus SM	13.0–18.0	15.5	0.04–10.00	0.10–0.25	0.175	Jones et al. (1974); Kuhlmann et al. (1981); Person LeRuyet et al. (1981); Paulsen et al. (1985); Quantz (1985)
Pseudopleuronectes americanus PA	2.0–10.0	6.0	0.01–1.45	0.02–0.14	0.080	Laurence (1975,1977); Buckley (1982); Cetta and Capuzzo (1982)
Achirus lineatus AL	28.0	28.0	0.01–0.20	0.16–0.33	0.245	Houde (1977d, 1978); Houde and Schekter (1981)
Solea solea SS	17.0–19.0	18.0	0.30–8.00 (wet wts)	0.10–0.21	0.155	Girin (1979); Fuchs (1982); Gatesoupe and Luquet (1982)

Estimated G increased from 0.04 at 5°C to 0.28 at 30°C. The Q_{10}, calculated from the predicted G, was 2.11 over the range 5°–30°C.

Some species deviated considerably from the average regression relationship (Fig. 1; Table 2). For example, Pacific mackerel, *Scomber japonicus*, larvae had a high growth rate; however, Atlantic mackerel, *S. scombrus*, did not deviate much from the regression line. Northern anchovy, *Engraulis mordax*, also had relatively high growth rate, while herring, *Clupea harengus*, Pacific hake, *Merluccius productus*, and milkfish, *Chanos chanos*, had lower than expected growth rates for their respective temperature. The observed variation in growth rates was greatest at high temperature (Fig. 1), indicating that fish larvae at high temperatures and, more generally, in low latitudes have potentially more variable growth rates than do larvae at low temperatures from high latitudes.

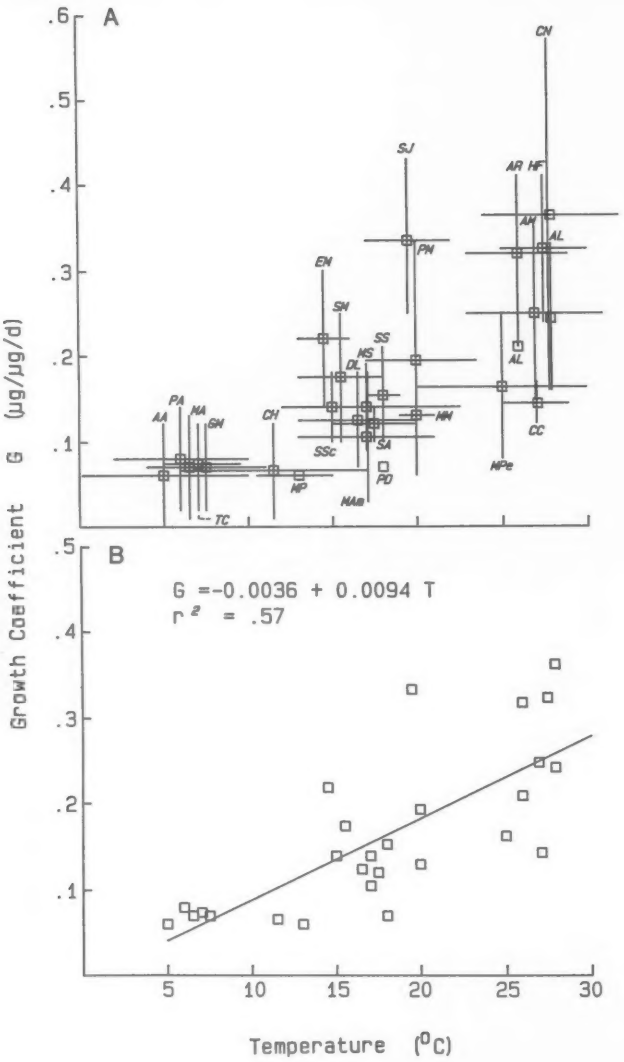

FIGURE 1.—Weight-specific growth coefficients (G) of marine fish larvae in relation to temperature (T). A. Ranges and midpoints of reported G and T values. Data, letters designating species and references are from Table 2. B. Regression relationship of midpoint G on midpoint T.

Stage Duration

Larval stage duration ranged from 10 days to >550 days, based on the reported growth rates (Table 3; Fig. 2). The regression relationship for 27 species indicated that stage duration (D) declines rapidly as temperature (T) increases.

$$D = 952.5T^{-1.0752}$$

$$r^2 = 0.70 \qquad S_b = 0.1418. \qquad (2)$$

Predicted stage duration ranged from 25 days at 30°C to >165 d at 5°C. The variability in stage duration was greatest at low tempera-

TABLE 3.—Estimated larval stage durations (D) from laboratory- and field-estimated growth rates, and weights at metamorphosis for marine fish larvae. Temperatures (T), and midpoints of D and T also are given. Values were derived from published results cited for each species in Table 1.

Species	Temperature		Hatch and metamorphosis dry weight (mg)		Stage duration (d)	
	Range	Midpoint	W_0	W_m	Range	Geometric midpoint
Clupea harengus CH	6.0–17.0	11.5	0.090	25.0	46.9–>550	160.6
Chanos chanos CC	25.0–29.0	27.0	0.05	25.0	36.6–51.8	43.5
Anchoa lamprotaenia ALa	26.0	26.0	0.02	25.0	34.0	34.0
Anchoa mitchilli AM	23.0–31.0	27.0	0.015	25.0	21.2–49.5	32.4
Engraulis mordax EM	13.0–16.0	14.5	0.020	25.0	23.8–50.9	34.8
Gadus morhua GM	4.0–11.0	7.5	0.050	7.0	41.2–247.1	100.9
Melanogrammus aeglefinus MA	4.0–9.0	6.5	0.070	7.0	35.4–460.5	127.7
Merluccius productus MP	10.5–15.0	13.0	0.04	7.0	88.0	88.0
Theragra chalcogramma TC	5.0–9.5	7.0	0.04	10.0	42.5–276.1	108.3
Menidia menidia MM	19.0–21.0	20.0	0.10	10.0	35.4	35.4
Menidia peninsulae MP	20.0–30.0	25.0	0.03	10.0	23.2–72.6	41.0
Morone americana MAm	13.0–21.0	17.0	0.02	10.0	34.5–207.2	84.5
Morone saxatilis MS	10.0–22.5	17.0	0.20	15.0	22.7–48.0	33.0
Dicentrarchus labrax DL	13.0–20.0	16.5	0.06	10.0	28.4–73.1	45.6
Haemulon flavolineatum HF	~25.0–~30.0	~27.5	~0.02	~7.0	14.3–24.4	18.7
Archosargus rhomboidalis AR	23.0–29.0	26.0	0.015	7.0	15.0–29.3	21.0
Pagrus major PM	17.0–23.5	20.0	0.01	7.0	19.9–109.2	46.6
Sparus aurata SA	15.0–20.0	17.5	0.02	7.0	41.8–58.6	49.5
Cynoscion nebulosus CN	24.0–32.0	28.0	0.02	7.0	10.3–36.6	19.4
Ammodytes americanus AA	0.0–10.0	5.0	0.04	10.0	46.0–>550	159.1
Scomber japonicus SJ	17.0–22.0	19.5	0.035	10.0	13.2–22.6	17.3
Scomber scombrus SSC	15.0	15.0	0.05	10.0	29.4–53.0	39.5
Paralichthys dentatus PD	18.0	18.0	~0.05	~7.0	98.8	98.8
Scophthalmus maximus SM	13.0–18.0	15.5	0.04	20.0	24.9–62.1	39.3
Pseudopleuronectes americanus PA	2.0–10.0	6.0	0.01	1.0	32.9–230.3	87.0

TABLE 3.—*Continued.*

Species	Temperature		Hatch and metamorphosis dry weight (mg)		Stage duration (*d*)	
	Range	Midpoint	W_0	W_m	Range	Geometric midpoint
Achirus lineatus AL	28.0	28.0	0.101	2.0	16.0–33.1	23.0
Solea solea SS	17.0–19.0	18.0	0.05	8.0	24.2–50.8	35.1

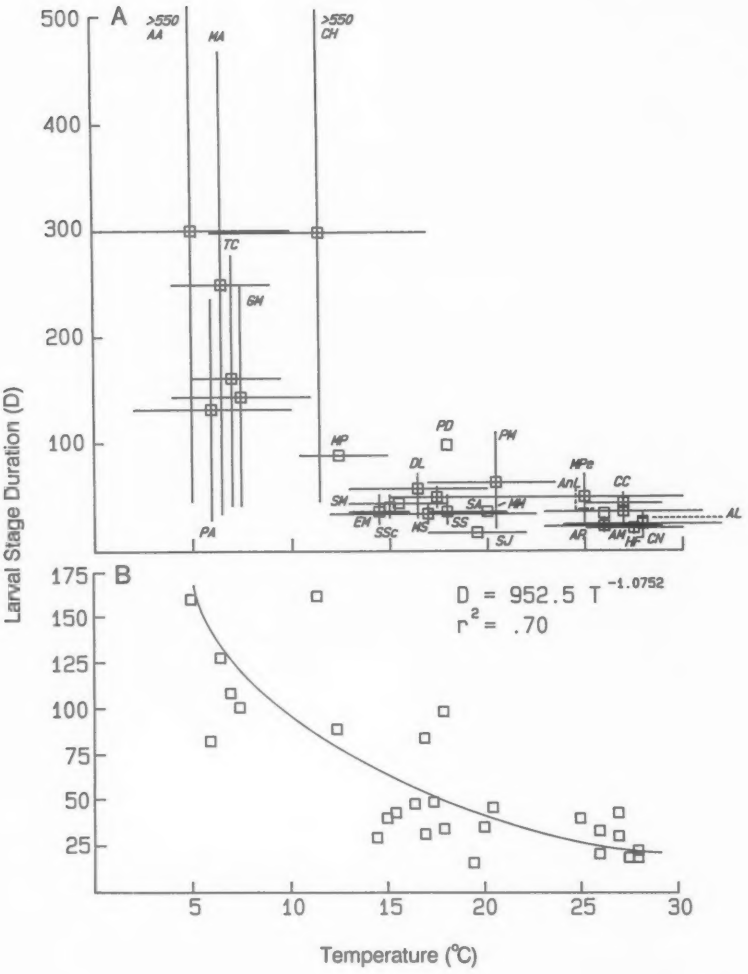

FIGURE 2.—Stage durations (D) of marine fish larvae in relation to temperature (T). A. Ranges and midpoints of D and T values. Data and letters designating species are from Table 3. References are in Table 1. B. Regression relationship of geometric midpoint D on midpoint T.

tures (Fig. 2), indicating more scope for stage duration at low temperatures and presumably in high latitudes. This result was opposite to that observed for growth rate, in which there was more variability at high temperatures (Fig. 1).

Mortality

Mortality coefficients of feeding-stage larvae reported for 22 species ranged from $Z = 0.01$ to 0.69 d^{-1}, equivalent to 1–50% d^{-1} mortality rates (Table 4; Fig. 3). Predicted mortality rate (Z) increased approximately 0.01 per degree increase in temperature (T).

$$Z = 0.0256 + 0.0123\,T$$

$$r^2 = 0.41 \qquad S_b = 0.0034. \qquad (3)$$

Estimated Z increased from 0.09 at 5°C to 0.40 at 30°C.

Although quite variable among species, the relationship between mortality rate and temperature is significant ($P < 0.01$). Only Atlantic mackerel appeared to be an outlier from the regression line (Fig. 3); its observed mortality rate was higher than expected for species in the 15–20°C range.

Relationship Between Mortality and Growth Rates

The derived relationship between mortality rate (Z) and growth rate (G) for marine fish larvae was

$$Z = 0.0303 + 1.3085\,G. \qquad (4)$$

Also, from predicted G and Z in Equations (1) and (3), it is apparent that the ratio G/Z increases at high T.

T (°C)	$\hat{G}$	$\hat{Z}$	G/Z
5	0.043	0.087	0.494
15	0.137	0.210	0.652
30	0.278	0.395	0.704

Despite the elevated mortality rates suffered by marine fish larvae at high temperatures, their growth potential may allow such larval populations to accumulate biomass and to survive at relatively high rates when feeding conditions are favorable.

Net Survivorship

Predicted net survival at metamorphosis increased by an approximate factor of nine as temperature increased from 10° to 30°C.

	10°C	*20°C*	*30°C*
G (d^{-1})	0.0904	0.1844	0.2784
D (d)	80.11	38.02	24.58
Z (d^{-1})	0.1486	0.2716	0.3946
100 N_{met} (%)	0.0007	0.0033	0.0061

The effects on N_{met} of a 10% decline in G, a 10% increase in Z, or a combination of 10% decline in G and 10% increase in Z were large.

G *declines 10%*

	10°C	*20°C*	*30°C*
G (d^{-1})	0.0814	0.1660	0.2506
D (d)	88.97	42.23	27.31
Z (d^{-1})	0.1486	0.2716	0.3946
100 N_{met} (%)	0.0002	0.0010	0.0021

Z *Increases 10%*

	10°C	*20°C*	*30°C*
G (d^{-1})	0.0904	0.1844	0.2784
D (d)	80.11	38.02	24.58
Z (d^{-1})	0.1635	0.2988	0.4341
100 N_{met} (%)	0.0002	0.0012	0.0023

G *declines 10% and* Z *increases 10%*

	10°C	*20°C*	*30°C*
G (d^{-1})	0.0814	0.1660	0.2506
D (d)	88.97	42.23	27.31
Z (d^{-1})	0.1635	0.2988	0.4341
100 N_{met} (%)	0.00005	0.0003	0.0007

Effects on percent larval survival at metamorphosis (100 N_{met}) of declining growth rates or increasing mortality rates are greater at low than at high temperatures, a consequence of the long stage durations at low temperature and their dependency on growth rate. Calculated ratios of N_{met} from the examples given above, termed relative survival, compared to those *expected* from the regression relationships at average G, D and Z, are

	Relative Survival		
Example	*10°C*	*20°C*	*30°C*
Expected G, D, Z	1.00	1.00	1.00
G declines 10%	0.27	0.32	0.34
Z increases 10%	0.30	0.36	0.38
G declines 10% and Z increases 10%	0.07	0.10	0.12

TABLE 4.—Instantaneous daily mortality coefficients (Z) from field estimates of reported mortality rates of marine fish larvae in relation to temperatures (T). Estimates here are for feeding-stage larvae only.

Species	Temperature (°C)		Mortality coefficient (Z)		References
	Range	Midpoint	Range	Midpoint	
Alosa sapidissima AS	19.0–23.0	21.0	0.11–0.30 (10–18 mm larvae)	0.210	Crecco et al. 1983
Clupea harengus CH	6.0–17.0	11.5	0.01–0.46	0.235	Graham and Townsend 1985; McGurk 1986; Lough et al. 1985
Etrumeus teres ET	18.0–26.5	22.5	0.13	0.130	Houde 1977a
Harengula jaguana HJ	21.0–31.0	26.0	0.28	0.280	Houde 1977c
Opisthonema oglinum OO	22.5–30.5	26.5	0.21–0.26	0.235	Houde 1977b
Sardinella aurita SA	21.0–27.0	24.0	0.45	0.450	Conand 1977
Sardinops melanosticta SM	11.1–19.1	15.1	0.13	0.130	Nakai and Hattori 1962
Sardinops sagax SS	15.5–18.0	16.4	0.10	0.100	Lenarz 1973
Anchoa mitchilli AM	24.0–31.0	27.5	0.30–0.45	0.375	Leak and Houde 1987
Engraulis japonica EJ	16.0–18.0 (from other literature)	17.0	0.30	0.300	Hiyashi 1966
Engraulis mordax EM	12.0–20.0	16.0	0.16–0.22	0.190	Hewitt and Methot 1982; Smith 1985; McGurk 1986
Melanogrammus aeglefinus MA	4.0–9.0	6.5	0.11	0.110	Jones 1973
Micromesistius poutassou MP	2.0–15.0 (from other literature)	8.5	0.15	0.150	Bailey 1974
Morone saxatilis MS	12.0–22.5	17.0	0.13–0.21	0.170	Dey 1981
Trachurus symmetricus TS	15.0–16.5	16.0	0.18 (rate estimated at 30 d posthatch)	0.180	Hewitt et al. 1985
Archosargus rhomboidalis AR	22.0–29.0	25.5	0.43	0.430	Chavance et al. 1984
Cynoscion nebulosus CN	24.0–31.0	27.5	0.36–0.64	0.500	Peebles and Tolley 1988
Scomber japonicus SJ	13.0–23.0	18.0	0.14	0.140	Watanabe 1970
Scomber scombrus SSc	14.0–20.0	17.0	0.35–0.69	0.520	Sette 1943; Kendall and Gordon 1981; Ware and Lambert 1985
Sebastes spp. Ssp	3.5–12.5	8.0	0.05–0.07	0.060	Anderson 1984
Pleuronectes platessa PP	1.0–8.0	4.5	0.02–0.08	0.050	Harding and Talbot 1973; Bannister et al. 1974; Harding et al. 1978
Pseudopleuronectes americanus PA	3.0–14.0	8.5	0.23	0.230	Pearcy 1962a, 1962b

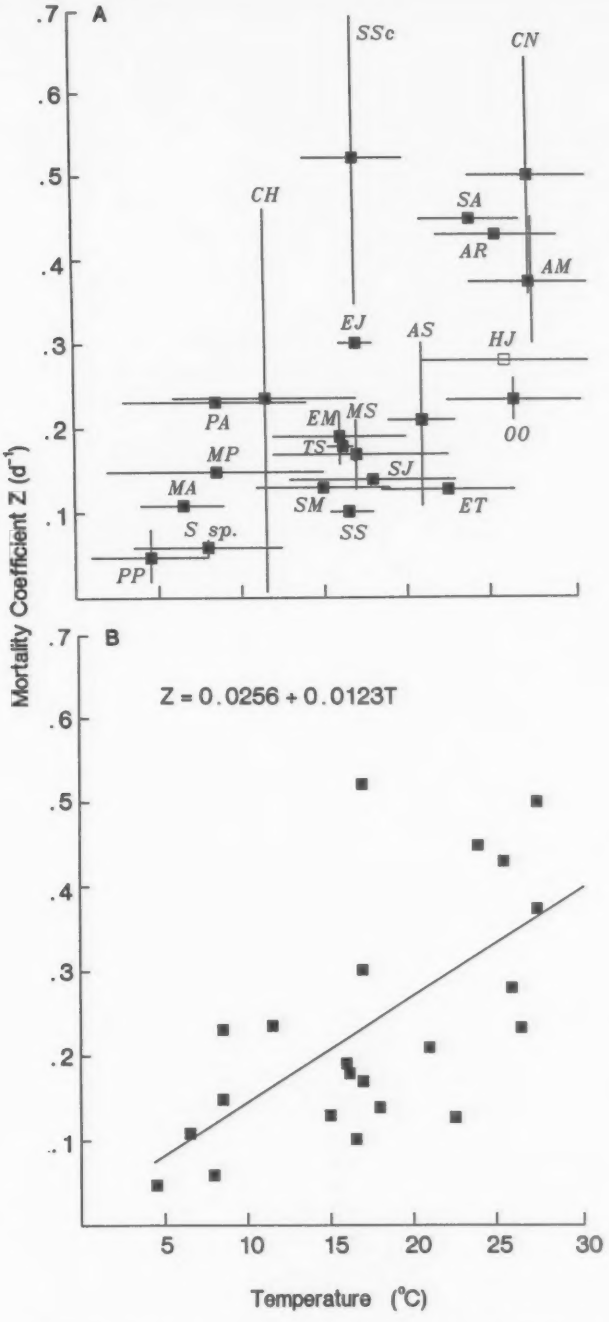

FIGURE 3.—Instantaneous mortality coefficient (Z) of marine fish larvae in relation to temperature (T). A. Ranger and midpoints of Z and T values. Data, letters designating species and references are from Table 4. B. Regression relationship of midpoint Z on midpoint T.

It is important to note that a 10% change in either Z or G will have potentially large effects on survivorship at any temperature.

Growth Efficiency and Ingestion

There was no significant relationship between growth efficiency and temperature (Table 5; Fig. 4) for 10 species where data were adequate for analysis. Mean K_1, with 0.95 confidence limits, is 0.29 ± 0.06, a value equal to that of juvenile, carnivorous fishes (Brett and Groves 1979). One species, European seabass, *Dicentrarchus labrax*, had reported K_1 well above the mean. Two species, winter flounder, *Pseudopleuronectes americanus*, and summer flounder, *Paralichthys dentatus*, had K_1 below the mean. For some species, a large range of potential K_1 was reported (Fig. 4), indicating that estimates of growth efficiency may vary widely in relation to environment, physiology, and perhaps the method used to calculate it.

Estimated weight-specific ingestion rates were determined for the 10 species from the relationship $I = G/K_1$. For these species there is a good relationship between ingestion rate (I) and growth rate (G) (Fig. 5).

$$I = 0.1203 + 2.8691\,G$$

$$r^2 = 0.80 \qquad S_b = 0.5140. \qquad (5)$$

There was no detectable relationship between ingestion and temperature for these 10 species because of the highly variable growth rates and growth efficiencies that were reported. However, given the relationship between G and T (Equation (1)) and the mean value for K_1, an expression describing a general relationship between I and T for marine fish larvae was derived.

$$I = G/K_1 \qquad I = (-0.0036 + 0.0094\,T)/0.29,$$

yielding

$$I = -0.0125 + 0.0326\,T. \qquad (6)$$

Thus, to attain the expected growth rate, ingestion must increase with temperature. A threefold increase in weight-specific ingestion rate is required to meet the demands of expected growth at 30°C compared with that needed at 10°C. The result demonstrates that tropical fish larvae or those living at high summer temperatures must ingest relatively large amounts

TABLE 5.—Gross growth efficiencies (K_1) of marine fish larvae from laboratory experiments.

Species	Temperature (°C) Range	Temperature (°C) Midpoint	Mortality coefficient (Z) Range	Mortality coefficient (Z) Midpoint	References
Clupea harengus CH	7.0–9.0	8.0	<0.10–0.62	0.360	Checkley 1984; Kiorboe and Munk 1986; Kiorboe et al. 1987
Anchoa mitchilli AM	26.0	26.0	[1]0.11–0.32	0.215	Houde and Schekter 1981, 1983
Engraulis mordax EM	15.5	15.5	0.24–0.46	0.350	Theilacker 1987
Dicentrarchus labrax DL	18.0–19.0	18.5	0.26–0.57	0.415	Barahona-Fernandez and Girin 1977
Morone saxatilis MS	18.0–21.0	19.5	0.14–0.32	0.230	Eldridge et al. 1982; Chesney 1986; Tuncer 1988
Archosargus rhomboidalis AR	23.0–29.0	26.0	[1]0.21–0.41	0.310	Stepien 1976; Houde and Schekter 1981, 1983
Scomber japonicus SJ	17.0–22.0	19.5	0.20–0.44	0.320	Hunter and Kimbrell 1980
Paralichthys dentatus PD	18.0	18.0	0.05–0.24	0.145	Buckley and Dillman 1982
Pseudopleuronectes americanus PA	6.0–8.0	7.0	0.05–0.33	0.190	Laurence 1977; Cetta and Capuzzo 1982
Achirus lineatus AL	28.0	28.0	[1]0.13–0.52	0.325	Houde and Schekter 1981, 1983

[1]The highest values reported by Houde and Schekter (1981) were not included here, based on their note that these values were in error.

of food to grow at their observed, average rates. Because it depends on the relationship between growth rate and temperature, the Q_{10} for ingestion rate in the 5°–30°C range is 2.11, the same as that calculated for growth rate.

From the estimates of weight-specific ingestion (Table 6), the numbers of food organisms were calculated that would satisfy the growth requirements of first-feeding larvae of the 10 species. The number of required prey is directly proportional to growth rate and to W_0, the initial dry weight of a larva, and is inversely propor-

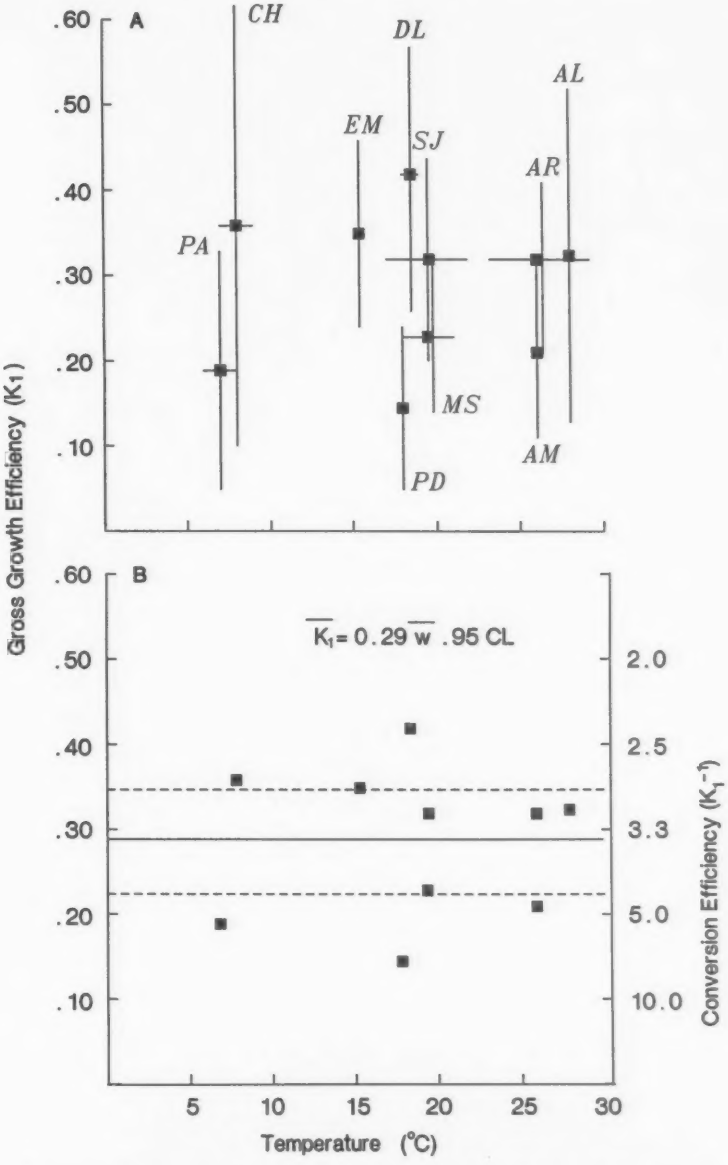

FIGURE 4.—Gross growth efficiency (K_1) and conversion efficiency (K_1^{-1}) of marine fish larvae in relation to temperature (T). A. Ranges and midpoints of K_1 and T values. Data, letters designating species and references are from Table 5. B. Mean K_1 and 0.95 confidence limits from the attempt to regress midpoint K_1 on midpoint T. There was no significant regression of K_1 on T.

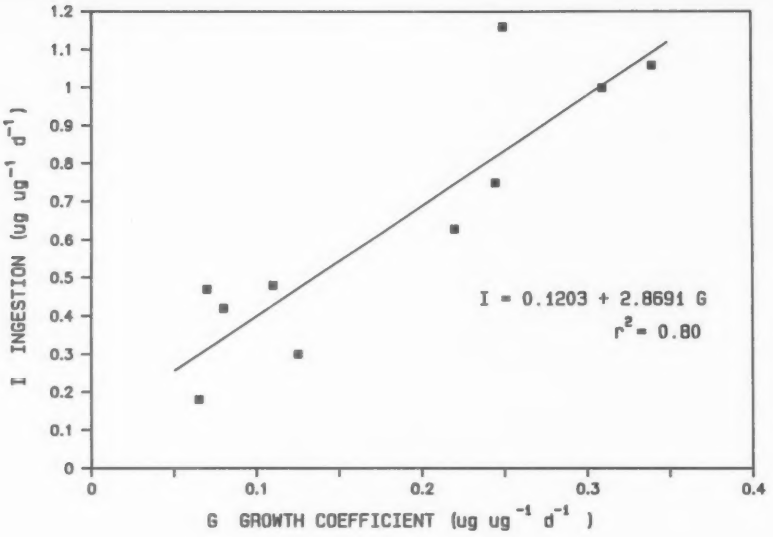

FIGURE 5.—Weight-specific ingestion rates (I) of marine fish larvae in relation to weight-specific growth coefficient (G). Data derived from Tables 2 and 5.

TABLE 6.—Estimated numbers of 0.25 μg dry weight food particles required by first-feeding marine fish larvae to meet their reported mean growth rates. Required total ingestion and weight-specific ingestion (i.e., number of particles per μg of growth) are given. Estimates were calculated from the G and K_1 values derived from published literature (see Tables 2, 4).

Species	Midpoint temperature (°C)	Midpoint G (μg μg^{-1} d^{-1})	Midpoint K_1	Initial larval weight (μg)	Daily weight increment (μg)	Number of 0.25 μg particles required (d^{-1})	Weight-specific ingestion (number μg^{-1}) d^{-1}
Clupea harengus CH	11.5	0.065	0.360	80	5.2	57.8	11.12
Anchoa mitchilli AM	27.0	0.250	0.215	10	2.5	46.5	18.60
Engraulis mordax EM	14.5	0.220	0.350	20	4.4	50.3	11.44
Dicentrarchus labrax DL	16.5	0.125	0.415	90	11.3	108.9	9.64
Morone saxatilis MS	17.0	0.110	0.230	200	22.0	382.8	17.40
Archosargus rhomboidalis AR	26.0	0.310	0.310	10	3.1	40.1	12.92
Scomber japonicus SJ	19.5	0.340	0.320	30	10.2	127.7	12.52
Paralichthys dentatus PD	18.0	0.070	0.145	~50	3.5	96.6	27.59
Pseudopleuronectes americanus PA	6.0	0.080	0.190	10	0.8	16.8	21.05
Achirus lineatus AL	28.0	0.245	0.325	10	2.5	30.2	12.32

tional to gross growth efficiency. Required prey of 0.25 μg dry weight (the approximate weight of a 100–200 μm width copepod nauplius) varied more than twentyfold, ranging from 17 to 383 d^{-1} among the 10 species (Table 6). Marine fish larvae must ingest 15.3 prey of 0.25 μg dry weight (15.3 ± 3.9 with 0.95 confidence limit) to attain a 1 μg increase in dry weight. To the extent that 0.25 μg either underestimates or overestimates the mean weight of a prey for a species of fish larva, the required numbers of prey were either overestimated or underestimated.

Metabolism

Weight-specific oxygen uptakes of feeding-stage larvae of 13 species ranged from 0.3 to 44.9 μL/mg/h and increased with temperature. All of the values, except those for haddock, *Melanogrammus aeglefinus*, which were considered outliers, were used in the regression describing the relationship between oxygen uptake (Q_{O_2}) and temperature (T) (Table 7; Fig. 6).

$$Q_{O_2} = 2.3973 + 0.2187\,T$$

$$r^2 = 0.39 \qquad S_b = 0.0870. \qquad (7)$$

The relationship was significant ($P = 0.025$), but the fit was not as good as those of the other regressions. In the 5°–30°C range, Q_{10} was 1.46, a value lower than that calculated for growth and ingestion rates.

After rearranging and substituting Equation (1) into Equation (7), an expression between oxygen uptake (Q_{O_2}) and growth rate (G) was derived.

$$Q_{O_2} = 2.2472 + 23.5000\,G \qquad (8)$$

From this relationship it can be seen that for growth rate in the sixfold range of 0.05–0.30, oxygen uptake varied only by a factor of 2.7.

Energy Budgets

There were substantial effects of temperature on the calculated energy budgets. Weight-specific ingestion rate increased threefold in the 10C°–30°C range (Table 8). Numbers of calories increased in all budget components as temperature increased. The relative contributions of each budget component show that growth remained constant, a consequence of gross growth efficiency being constant over all temperatures, and that relative metabolism declined at higher temperatures. Assimilation efficiencies declined from 77.1% at 10°C to 59.8% at 30°C. Net growth efficiencies, K_2, increased from 37.2% at 10°C to 48.1% at 30°C. Fecal energy increased twofold, from 22.9% at 10°C to 40.2% at 30°C.

DISCUSSION

Predicted growth and mortality rates of marine fish larvae increase by approximately 0.01 per degree in temperature, implying large differences in developmental times and daily probabilities of death in larvae that are hatched in either warm or cold seas. The very high growth and mortality rates at the high temperatures in tropical latitudes indicate fast turnovers of larval populations compared with the longer turnover times expected in temperate seas. In reviewing mortality of marine organisms in relation to their size, Peterson and Wroblewski (1984) and McGurk (1986) noted the exceptionally high mortality rates of marine fish eggs and larvae and discussed some probable reasons and consequences. McGurk (1986) believed that patchiness and susceptibility to predation explained the relatively high rates of mortality. The analyses presented here demonstrate that the rates not only are high but that they vary predictably with temperature. Based on the species that are represented, the results are presumed to represent a latitudinal trend as well as to be seasonally significant. More than fourfold differences in the expected mortality rates of marine fish larvae can be attributed to environmental temperature, without considering effects of larval size, in the 5°–30°C range. Expected weight-specific growth rates of fish larvae also were demonstrated to be six times higher at temperatures in tropical seas (30°C) than at temperatures in cold seas (5°C).

A consequence of declining temperature is an exponential increase in predicted larval stage duration (Fig. 2). Stage durations for larvae that develop at ≤8°C exceed 100 days, while larvae that develop at the 25°–30°C temperatures in tropical seas, metamorphose in ≤30 days. More importantly, there is a relatively large increase in its potential variability as stage duration increases. The highest variability in growth rate is observed in species that develop at high temperature (Fig. 1), but the highest variability in stage duration is observed at low temperature. Consequently, small changes in growth rate can

TABLE 7.—Weight-specific oxygen consumptions (Q_{O_2}) of marine fish larvae. Values given are for feeding-stage larvae. Some Q_{O_2} values were calculated from oxygen uptake on larval weight regressions if these were given by the authors.

Species	Temperature (°C) Range	Midpoint	Q_{O_2} (μL mg^{-1} h^{-1}) Range	Midpoint	References
Clupea harengus CH	5.0–18.0	11.5	0.30–5.00	2.65	Holliday et al. 1964; DeSilva and Tytler 1973; Eldridge et al. 1977; Almatar 1984; Kiorboe et al. 1987
Sardinops sagax SS	14.0	14.0	1.30–2.70	2.00	Lasker and Theilacker 1962
Anchoa mitchilli AM	26.0	26.0	4.00–8.20	6.10	Houde and Schekter 1983
Engraulis mordax EM	16.0–17.0	16.5	3.16–7.74	5.45	Theilacker and Dorsey 1980; Theilacker 1987
Gadus morhua GM	4.0–10.0	7.0	1.00–8.87	4.95	Laurence 1978; Davenport and Lonning 1980; Solberg and Tilseth 1984
Melanogrammus aegleinus MA	4.0–9.0	6.5	4.90–44.90	[1]24.90	Laurence 1978
Merluccius productus MP	8.0–15.0	11.5	4.50–12.10	8.30	Bailey 1982
Morone saxatilis MS	18.0	18.0	3.60–7.60	5.60	Eldridge et al. 1982
Archosargue rhomboidalis AR	26.0	26.0	5.6–11.03	8.32	Houde and Schekter 1983
Scomber japonicus SJ	18.0–22.0	20.0	6.10–11.4	8.75	Hunter and Kimbrell 1980
Pleuronectes platessa PP	5.0–18.0	11.5	1.10–5.98	3.54	DeSilva and Tytler 1973; Almatar 1984
Pseudopleuronectes americanus PA	2.0–8.0	5.0	1.80–8.00	4.90	Laurence 1975; Cetta and Capuzzo 1982
Achirus lineatus AL	28.0	28.0	2.00–19.70	10.85	Houde and Schekter 1983

[1]These values were calculated from the respiration on larval weight regressions in Laurence (1978). The values seem inordinately high and were not used in deriving the Eq. 7 relationship between Q_{O_2} and temperature.

TABLE 8.—Average energy budgets of first-feeding marine fish larvae derived from the growth, metabolism and growth efficiency data in the published literature. Absolute and relative (i.e. percent) budgets are presented for 10°, 20°, and 30°C. I = ingestion and G = growth (both assumed to have equivalencies of 5,000 cal g^{-1}). M = metabolism (converted from Q_{O_2} to energy units by the oxycalorific equivalent of 0.00463 cal μL^{-1} O_2). F = feces (calculated by difference). Budget is $I = G + M + F$. $K_1 = G/I$ $K_2 = G/(G + M)$ $A = (G + M)/I$.

Temperature (°C)	Absolute budget (cal μg^{-1} d^{-1})	Relative budget (%)	K_1	K_2	A
10	0.00157 = 0.00045 + 0.00076 + 0.00036	100 = 28.7 + 48.4 + 22.9	0.287	0.372	0.771
20	0.00320 = 0.00092 + 0.00113 + 0.00115	100 = 28.7 + 35.3 + 36.0	0.287	0.449	0.641
30	0.00483 = 0.00139 + 0.00150 + 0.00194	100 = 28.7 + 31.1 + 40.2	0.287	0.481	0.598

induce large changes in stage duration when temperature is low, a result that may significantly affect the recruitment process.

Within a species gross growth efficiency varies inversely in relation to ingestion (Checkley 1984; Kiorboe et al. 1987), and it probably varies in relation to other environmental factors as well. But, on average, the calculated gross growth efficiency for marine fish larvae equaled 0.29 ± 0.06 and there is no apparent relationship to temperature. It is noteworthy that the mean gross growth efficiency calculated for marine fish larvae is identical to that reported for juvenile carnivorous fishes (Brett and Groves 1979). Because growth efficiency does not increase, larvae at high temperatures must attain fast growth through increased food consumption. The derived relationship between ingestion and temperature indicates that ingestion must increase nearly threefold to support average growth at 30°C compared to 10°C.

Values of gross growth efficiency exceeding

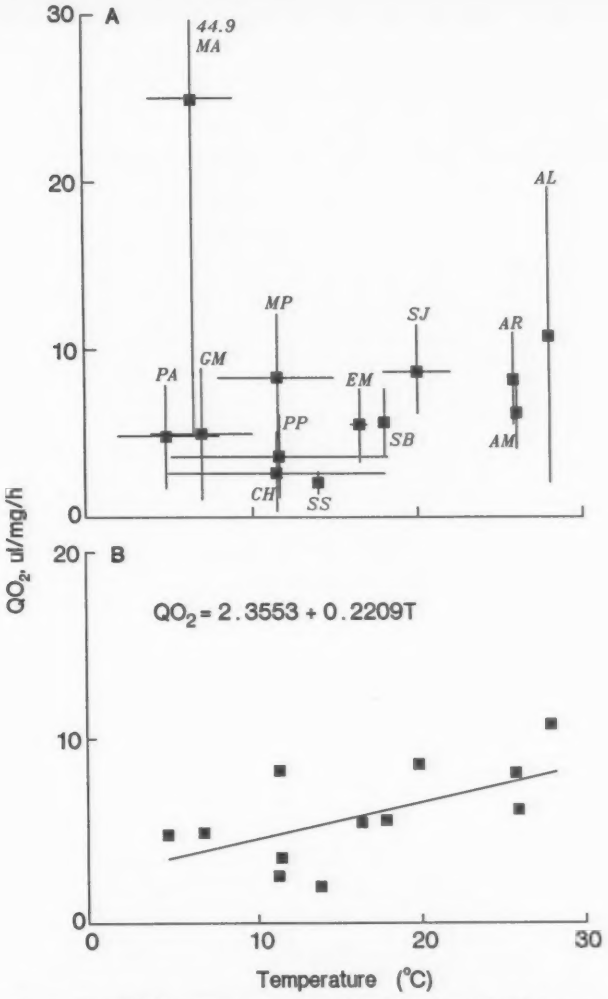

FIGURE 6.—Weight-specific oxygen uptake (Q_{O_2}) of marine fish larvae in relation to temperature (T). A. Ranges and midpoints of Q_{O_2} and T values. Data, letters designating species and references are from Table 7. B. Regression relationship of midpoint Q_{O_2} on midpoint T. The data point for haddock (i.e., MA) is not included in the regression.

0.50 for marine fish larvae have been reported, e.g., in *C. harengus* (Checkley 1984; Kiorboe et al. 1987). Kiorboe et al. argued that herring, and possibly fish larvae in general, may be operating near peak growth and assimilation efficiency, but most published estimates indicate that larvae are no more efficient than juvenile fishes or other fast-growing animals. Boehlert and Yoklavich (1984) obtained assimilation efficiencies for Pacific herring, *C. harengus pallasi*, larvae in the range of 40–60%. This implies that gross growth efficiency was considerably lower, because assimilation efficiency includes energy of metabolism as well as growth.

Weight-specific oxygen consumption increases slowly in relation to temperature compared to the observed increase in growth rate. Rombough (1988) noted that the Q_{10} for oxygen uptake by individual species of fish eggs and larvae ranges from 1.5 to 4.9, averaging 3.0. These values are considerably higher than the Q_{10} of 1.46 estimated here as the among species temperature (presumed latitudinal) effect on marine fish larvae. Still, fish larvae in warm seas have a

higher oxygen demand than larvae in colder seas. If gross growth efficiency is constant in relation to temperature, then assimilation efficiency should decline as temperature increases, while net growth efficiency should increase. Based on the calculated energy budgets at 10°C, 20°, and 30°C (Table 8), predicted assimilation efficiency declined from 77.1% at 10°C to 59.8% at 30°C. Average assimilation efficiencies of larval fish generally are thought to be similar to or less than the 80% mean assimilation efficiency of juveniles (Brett and Groves 1979; Govoni et al. 1986). Net growth efficiency increased from 37.2% at 10°C to 48.1% at 30°C. The range of predicted values of larval net gross efficiency lies just above the 36% mean value reported for juvenile fishes (Brett and Groves 1979). Recently, Wieser et al. (1988) estimated the net growth efficiency for larvae of the freshwater *Rutilus rutilus* and indicated that it was high and independent of temperature in the 15°–20°C range. Inspection of their table 4 data indicates that the net growth efficiency did in fact increase by approximately 4% in the 5°C range of their experiments, a percentage similar to that predicted from the energy budget analysis for marine fish larvae.

The mean assimilation efficiency for marine fish larvae declined as temperature increased. There also is good evidence that both assimilation and gross growth efficiency of an individual species decline at high ingestion rates (Houde and Schekter 1981; Checkley 1984; Boehlert and Yoklavich 1984; Kiorboe et al. 1987; Theilacker 1987). The ability of larvae to capture prey, the feeding conditions, and environmental factors all affect assimilation and growth, as well as their variability. Nevertheless, the efficiencies predicted here and their relationships to temperature still are believed to describe important latitudinal effects.

Despite expected high mortality rates, average survivorship of larval cohorts at tropical temperatures was predicted to exceed that of cohorts at high latitude temperatures. This result is a consequence of the high growth rates and the relatively short stage durations that tropical larvae experience. While net survivorship to metamorphosis in tropical systems may be relatively high, the daily probability of death also is high. Unless larval food abundance is higher or tropical larvae are better able than high latitude larvae to feed on scarce prey, neither of which has been demonstrated, starvation or other "critical period" mortalities (sensu Hjort 1914) may be more probable in the tropics. Cohort survivorship is sensitive to small changes in mortality and growth rates in either tropical or high latitude systems. But, larval cohorts developing in high latitudes are likely to suffer proportionally greater declines from small decreases in growth rates or increases in mortality rates, a consequence of their extended larval stage duration. If even weak or sporadic density-dependent growth or mortality operates in the larval stage (Rothschild 1986), its effect could be substantial in high latitudes where the larval stage is long.

Based on this analysis, starvation of first-feeding larvae is hypothesized to be more likely in warm seas because of their relatively great ingestion requirement combined with low assimilation efficiency. If it were possible for fish larvae to live on a maintenance diet, they would face less risk of food-limitation. But, in laboratory experiments it has been observed that slow-growing larvae are less likely to survive (Laurence 1977; Houde and Schekter 1980, 1981). Estimates here indicate that approximately 15 food particles of 0.25 μg dry weight are required to produce 1 μg dry weight of larval growth. Tropical fish larvae that are growing 2–3 times as fast as larvae from cold seas, and which also have an elevated metabolism, must consume nearly three times as much prey to achieve average growth at ambient temperatures.

Average relationships reported here indicate that larval mortality rates exceed weight-specific growth rates. Morse (1989) also has examined the relationship among growth, mortality, and temperature for 26 species of North Atlantic fish larvae. He found that both growth rates and mortality rates increased with temperature. He concluded that the ratio of mortality rates to growth rates is less than 1.0 for most of those species, and suggested that, when ratios exceeded 1.0, gear avoidance is the possible cause. In my analysis I have accepted the possibility that mortality rates may exceed growth rates for teleost larvae, implying that there is a loss of biomass between the egg stage and metamorphosis in most species. The ratio of mortality rates to growth rates, based on the regression coefficients in the mortality rates on temperature and growth rates on temperature regressions is 1.31. Morse (1989) concluded that if larval growth rate is known, then mortality rates can be predicted because the two rates are correlated. This conclusion supports the obser-

vation that mortality rates potentially can be derived from relatively easy to obtain information on larval growth rate and its variability (Houde 1987). Before such estimates are possible, it will be necessary to explicitly determine the growth rates and mortality rates of many species to establish how reliable this approach might be.

Differences in spawning strategies of marine fishes may have evolved as a consequence of the different constraints on growth and survival of larvae from high and low latitudes. The constraints for low-latitude larvae, i.e., high mortality rates, high growth rates with attendant short stage duration, and required high ingestion, suggest that few larval cohorts will find the necessary local conditions conducive for growth and survival. In most cases cohorts will starve or be eaten. It is hypothesized that protracted spawning, serial spawning and frequent batch production of eggs, a common strategy in the tropics, will insure that some larval cohorts hatch during those brief periods when conditions favor the high growth rates that promote survival. In high latitudes, where spawning often is temporally and spatially confined, larvae have different constraints. There, both mortality and growth rates tend to be low, ingestion is relatively low, but stage duration is long and potentially very variable. Under such circumstances small changes in either mortality rates or growth rates can have major impacts on recruitment potential (Shepherd and Cushing 1980; Houde 1987). And, long larval stage durations also provide ample time for density-dependent mechanisms to develop which may regulate abundance and dampen fluctuations in stocks that originated from one or a few batch spawnings that occurred during a brief time. Under these conditions the timing of spawning (Cushing 1975) and the selection of favorable spawning sites (Iles and Sinclair 1982) by adults are critical to the recruitment success of a cohort.

Although density-dependent regulation in early life often is assumed, there is relatively little evidence that it does in fact play a major role in the egg and larval stage. Jones (1973), Cushing and Harris (1973), Ware (1975), and Shepherd and Cushing (1980) have modeled the recruitment process, demonstrating how density-dependent mortality and/or growth can regulate abundance. They have argued that regulation may be most effective in the larval stage. In support of those arguments, Savoy and Crecco (1988) have demonstrated that density-dependent mortality during the egg and larval stage may play a significant role in the regulation of anadromous American shad, *Alosa sapidissima*, populations. Based on analyses of larval life history characteristics reported here, if density-dependent regulation is significant, it seems more likely to be effective in high latitudes than in tropical seas. The long stage duration and its potential variability, caused by varying temperature or food availability, may promote competition or allow predators to aggregate, favoring density-dependent control. In contrast, because larval stage durations in tropical seas are short and less variable, the probabilities of competitive or predator-mediated, density-dependent effects seem less likely.

The production of multiple cohorts during protracted spawning by tropical fishes and by many summer spawners in higher latitudes is a bet-hedging strategy that will allow some daily-produced cohorts to experience conditions favorable for survival. Lambert (1984) and Lambert and Ware (1984) have proposed that single batch, demersal spawners in high latitudes (e.g., herring and capelin, *Mallotus villosus)* are more likely to produce easily discernible cohorts of larvae than are summer-spawning pelagic species (e.g., Atlantic mackerel, *Scomber scombrus*, and white hake, *Urophycis tenuis*) in the same region because the demersal spawners are characterized by waves of females that deposit eggs at discrete time intervals. They argued that, in the cases of herring and capelin, widely spaced cohort production represented bet-hedging by reducing potential intraspecific competition among larvae and by assuring that cohorts of prey would develop with cohorts of fish larvae (Jones 1973; Jones and Hall 1974). Lambert and Ware (1984) believed that Atlantic mackerel and white hake females spawned every 2–3 days and that spawning in such species would appear to be continuous during their summer spawning season. In agreement with that argument, it is hypothesized here that teleost stocks spawning at high temperatures are more likely to produce daily cohorts of eggs than are those stocks spawning at low temperatures because the larvae of warm-water stocks have short stage durations and are constrained by the necessity for high growth and by their high mortality rates. This point is supported by Lambert and Ware's (1984) figure 4, in which they show that when larval growth rates are high, as they are in the tropics and in many high-latitude summer spawners, the predicted time period between

cohorts is reduced to only a few days. Under such conditions tropical species may spawn frequently for long periods (Clarke 1987) as a mechanism to promote recruitment success.

Several attempts have been made to develop unifying theories that explain recruitment fluctuations and regulation, including the match-mismatch hypothesis (Cushing 1975), the stable ocean hypothesis (Lasker 1978; 1981), and the larval retention hypothesis (Iles and Sinclair 1982). None of these is entirely satisfying, given the diverse nature of teleost fishes and the environments in which they live. Miller et al. (1988) have demonstrated that interspecific variation in larval size is a strong determinant of growth rate and a predictor of starvation-induced mortality. Hunter (1981) also recognized that larvae could be classified by their relative first-feeding abilities as judged by mouth size and general morphology. Miller et al. (1988) and Hunter (1981) have demonstrated that larvae can be categorized by their morphology as starvation-prone or not. Here, it is demonstrated that temperature, and by implication latitude, exercises a strong influence on the energetics, growth, and mortality rates of marine fish larvae. Furthermore, it is proposed that these traits have favored selection of spawning strategies that have evolved in warm and cold seas.

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Comparison of the Mortality Rates of Pacific Sardine, *Sardinops sagax*, and Peruvian anchovy, *Engraulis ringens*, Eggs off Peru[1]

Paul E. Smith, Haydee Santander, and Juergen Alheit

ABSTRACT: Egg production and mortality rates were estimated for populations of Pacific sardine, *Sardinops sagax*, and Peruvian anchovy, *Engraulis ringens*, off north and central Peru for August to September 1981. Peruvian anchovy spawned in the entire inshore region, principally within 56 km (30 nmi) of the coast. The Pacific sardine spawned extensively in the northern and southern inshore regions but not in the central region. While spawning of the two species coincided at the regional scale, at the sample scale, the occurrence of eggs of the two species was statistically independent. The egg production rate of Peruvian anchovy was about double that of sardine. The mortality rate of Pacific sardine eggs was much higher than that of Peruvian anchovy. The egg mortality rates of Peruvian anchovy and Pacific sardine were unchanged at stations where Pacific sardine and Peruvian anchovy eggs occurred together, relative to where the two species' eggs occurred separately. Results of this study are used to evaluate cannibalism as a population limiting mechanism. Cannibalism accounts for about 30% of egg mortality in anchovy. Because of the schooling habit of sardines and anchovies, cannibalism, though large-scale, may not vary enough with population size to explain variations in recruitment.

In their review of clupeoid biology, Blaxter and Hunter (1982) emphasized the need to estimate instantaneous rates as the "only way to establish a satisfactory linkage between the fish and their environment." These instantaneous rates include production of spawn (Lasker 1985) and mortality rate of the eggs and larvae. Predation is thought to be an important cause of mortality, and one form of predation, cannibalism, has been proposed as a mechanism for establishing an upper limit to population density (Ricker 1954; Hunter and Kimbrell 1980; MacCall 1980; Alheit 1987; Pauly and Soriano 1987) of filter-feeding, pelagic spawning, schooling coastal pelagic fishes.

MacCall (1983) has described abundance as a composite of population density and geographic extent: northern anchovy, *Engraulis mordax*, appears to have a central area where density-dependent processes have their greatest effect on local density and a peripheral area where density-dependent processes are less important. Reductions of density in the central area result in contractions of the population to the central area for Pacific sardines, *Sardinops sagax*, (Murphy 1966) and northern anchovy (MacCall 1980). Off California both sardines and anchovy contract to the same area (Ahlstrom 1967).

Microstructure in the sea plays an important role in interaction of predator and prey (Lasker and Smith 1977) at the embryonic and larval stages (Smith 1973; Vlymen 1977; Theilacker 1987). There may also be rapid changes in the microstructure due to dispersal (Smith 1973; Smith and Hewitt 1985b). McGurk (1987) has proposed that small-scale pattern may make mortality rates proportional to patchiness rather than inversely proportional as originally suggested by Brock and Riffenburgh (1960).

Subsequent variations in recruitment may be caused by environmental influences on first-feeding larvae (Hjort 1926; Lasker 1975, 1978, 1981; Peterman and Bradford 1987), and recruitment is regulated by the interaction of growth and mortality rates of juveniles (Shepherd and Cushing 1979; Smith 1985; Butler 1987). Peterman et al. (1988) demonstrated that in a selected subset of years there was no relationship be-

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tween the abundance of northern anchovy larvae off California at 20 days of age and the recruitment at age 1. It had previously been shown that, for a shorter time series in the same habitat, Pacific sardine recruitment at two years old varied 15-fold, while the egg abundance in the year of origin for the same years varied only 3-fold (Smith 1978).

A major barrier to estimating egg mortality in pelagic schooling fish is the tendency of these fish to aggregate closely for external fertilization of spawn (Leong in press), presumably to conserve sperm and ensure high fertilization rates. The eggs are subsequently dispersed by turbulent diffusion (Smith 1973; Smith and Hewitt 1985a). Schooled spawning, with its spatially intense pattern, imposes a high sample variance on the younger eggs, and dispersal reduces the sample variance with time (Smith and Hewitt 1985a).

Precise estimation of survival and egg production rates requires large numbers of samples. The intensity of patchiness is indicated by the maximum values for egg counts. Smith (1973) observed that the concentration of Pacific sardine eggs off California was a maximum of 3,100 eggs/m^2, and Hunter (1980) observed that a concentration of 1 d old northern anchovy eggs was 4,600 per m^2. Walsh et al. (1980) reported the results of sample analyses of Peruvian anchovy eggs along the Peruvian coast. From five samples at lat. 10°S and seven samples at 15°S, they found a maximum value of 11,500 Peruvian anchovy eggs/m^2, and they also found Peruvian anchovy larvae at 100 and 200 per m^2. Santander et al. (1982) reported on Peruvian anchovy and Pacific sardine off Peru. For Peruvian anchovy, they found a maximum egg concentration of 107,376 eggs/m^2 (all ages). This count was from the largest of 911 ichthyoplankton tows with Peruvian anchovy eggs out of 4,028 Hensen net samples between 1966 and 1979. For Pacific sardine off Peru, the maximum egg concentration was 58,500 eggs/m^2 (H. Santander[2]). This count was from the same set of 4,028 tows.

Pacific sardine spawning off Peru has been essentially stable between 1978 and 1981 (Santander 1981). What are the implications for selection of spawning sites for the two pelagic spawners? Do the two species partition the environment into separate spawning areas or do they concentrate on oceanic sites favorable to both? What are the relative rates of egg production and mortality where they co-occur?

In this paper we describe regional and interspecific differences in egg production and mortality off Peru. The Peruvian anchovy data used for this paper have already been used for estimating egg production of the Peruvian anchovy population off north and central Peru (Santander et al. 1984). The Pacific sardine egg data off Peru are adequate for determining egg production per unit area, but contemporaneous adult reproduction rates are lacking; thus, sardine adult biomass has not been estimated.

METHODS

Cruise plan, sampling methods, laboratory methods, and data analysis have been described fully by Santander et al. (1984; an English version can be obtained from the author J. Alheit). Only a brief account of these methods is presented here.

The objective of the investigation was to encompass the Peruvian anchovy and Pacific sardine spawning grounds off northern and central Peru with an intensive grid of ichthyoplankton stations. The survey extended from Pisco (lat. 14°S) in the south to Punta Falsa (6°S) in the north. The background, a computer program for distributing the stations, and other technical details of the cruise plan are described in Smith et al. (1983). The sampling stations were distributed on transects perpendicular to the coastline. The inshore spacing of transects was 10 nmi. Thirty-five transects extended 30 miles offshore and 18 transects extended 90 miles offshore. On all transects the sampling stations were three miles apart. The total number of stations was 925. The area under investigation was subsequently divided into nine regions for some aspects of the analysis (Fig. 1).

Eggs were sampled with the CalVET net (CalCOFI vertical egg tow; Smith et al. 1985). Its mesh size was 333 μm, and its mouth area was 0.05 m^2. The net was towed vertically from a 70 m depth to the surface within 1 minute. The net filtered 3.5 m^3 of water.

Following sorting, the eggs were aged according to their developmental stage, the surface water temperature, and the time of day when the sample was collected. The following is a brief summary of the method for determining Peruvian anchovy egg production; a complete description of these techniques for northern anchovy is found in Picquelle and Stauffer (1985).

[2]H. Santander, Instituto del Mar del Peru, Apartado 22, Callao, Peru, unpubl. data.

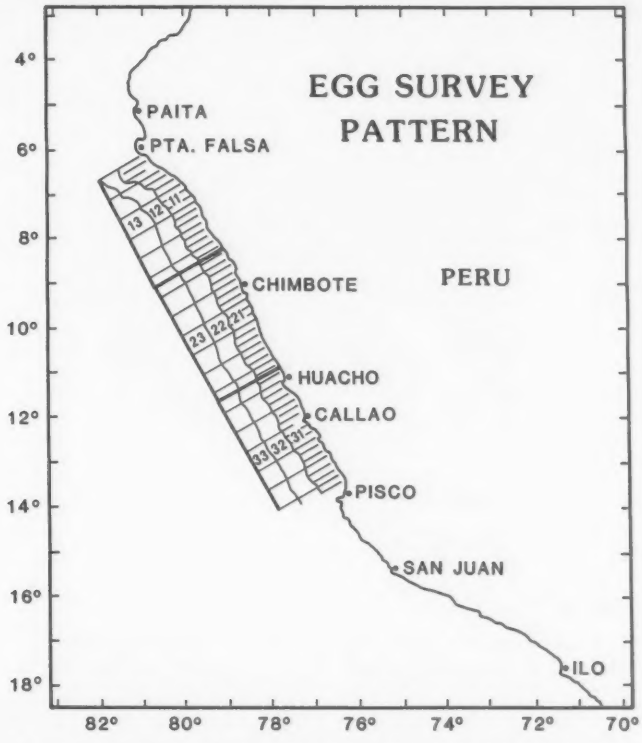

FIGURE 1.—Coastline of Peru and egg survey stations and statistical regions. Egg sampling stations are 3 miles apart in the cross-shelf plane. Regions for statistical summaries are coded. The first digit of each number refers to the north "1", central "2", or south "3" sectors of the coast. The second number refers to the inshore "1", offshore "2", or seaward "3" regions of each sector. In text, codes referred to as IMAR11, IMAR12, etc. to distinguish the codes from numbers. Original station positions and equations for plotting are in Smith et. al. (1983).

Anchovy and sardine eggs were grouped in 12 h intervals. Newly spawned eggs collected during the spawning interval and older eggs collected during hatching were eliminated from the calculations. The remaining egg counts were regressed on age to fit a mortality function of the egg data. The daily egg production was then estimated by zero intercept of the exponential mortality function. The following exponential model can be fit to the egg data by the nonlinear, least squares regression (Stauffer and Picquelle 1980[3]):

$$P_0 = P_i\, e^{-zt}$$

where P_0 = daily egg production;
P_i = number of eggs of age t_i sampled during the time interval t_i, t_{i+1};
t = time elapsed between spawning and the ith time interval; and,
Z = instantaneous daily rate of egg mortality.

The P_0 is the intercept of the exponential curve. The model assumes that all eggs are spawned and fertilized at an instant, that the eggs have a constant rate of mortality, and that the sampling was representative and includes all areas where eggs may be found.

RESULTS

Peruvian anchovy and Pacific sardine co-occur along the north and central coast of Peru

[3]Stauffer, G. D., and S. J. Picquelle. 1980. Estimates of the 1980 spawning biomass of the central subpopulation of northern anchovy. U.S. Dep. Commer., NOAA, NMFS SWFC Adm. Rep. LJ-80-09, 41 p.

(Santander 1981). In 1981, the Peruvian anchovy egg distribution was essentially continuous near the coast, with some extension offshore to 30 miles offshore of Chimbote (Fig. 2). In contrast, the Pacific sardine eggs occurred in two groups separated by about 120 nmi between Huacho and Chimbote. The Pacific sardine eggs extended farther offshore than Peruvian anchovy eggs and were not as abundant in the nearshore stations.

Of the 925 samples that were taken (Santander et al. 1984), 575 came from the inshore regions IMAR11, IMAR21, and IMAR31 (Fig. 1). Twenty-one percent of the samples in the inshore regions had both Peruvian anchovy and Pacific sardine eggs, 32% had only Peruvian anchovy eggs, 18% only Pacific sardine eggs, and 28% had neither Peruvian anchovy nor Pacific sardine eggs (Table 1).

There were fourfold fewer ½ d old Pacific sardine eggs per station in the samples with Pacific sardine eggs in the absence of Peruvian anchovy eggs as compared with Pacific sardine eggs per station when Peruvian anchovy eggs were also present (Table 2). By way of contrast, the Peruvian anchovy eggs appeared to be equally abundant, with or without Pacific sardine eggs in the sample. There appeared to be a trend of Pacific sardine egg abundance in absence of Peruvian anchovy eggs becoming proportionally less abundant with age, but the trend was mostly concealed by the high standard errors of the two categories. Of course these rates cannot be known precisely from exploratory data analysis; the absolute rates would have to result from specifically designed studies with higher precision.

On a regional basis, sardine egg production was highest in the northern region (IMAR11), negligible in the central region (IMAR21), and higher in the southern region (IMAR31, Table

TABLE 1.—Number (% in parentheses) of plankton hauls in which Peruvian anchovy, *Engraulis ringens*, and/or Peruvian sardine, *Sardinops sagax*, eggs occurred in the three inshore regions.

Region	Both anchovy and sardine	Anchovy only	Sardine only	Neither anchovy nor sardine	Total
IMAR11	51 (27)	26 (14)	65 (35)	45 (24)	187
IMAR21	34 (17)	91 (46)	18 (9)	54 (27)	197
IMAR31	36 (19)	69 (36)	22 (12)	64 (34)	191
Total	121 (21)	186 (32)	105 (18)	163 (28)	575

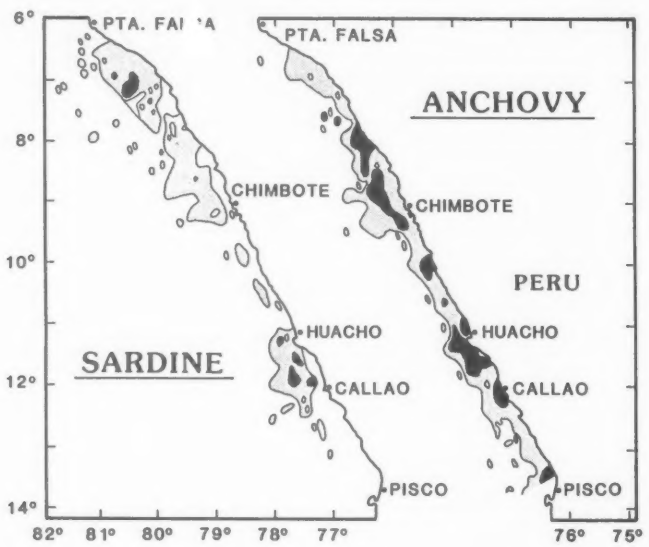

FIGURE 2.—Pacific sardine (left) and Peruvian anchovy (right) egg abundance in August to September 1981. For each species, shaded areas indicate where their eggs were taken at densities of 1–100 eggs/0.05 m^2, and black areas indicated 101 or more eggs/0.05 m^2. Peruvian anchovy data has also been mapped in units of eggs per square meter in Santander (1987, Map No. 78, p. 204).

TABLE 2.—Mean number of Peruvian anchovy, *Engraulis ringens*, and Pacific sardine, *Sardinops sagax*, eggs per station by age group. The age group code A1 refers to eggs aged in the first half of the first day after spawning; A2 refers to eggs aged in the second half of the first day; B1 refers to eggs aged in the first half of the second day; and B2 refers toe ggs aged in the second half of the second day. "All" refers to all stations where that species' eggs were present. Only the inshore regions (IMAR11, IMAR 21, IMAR31) combined were considered for estimation of these parameters. "Both" refers to those stations where eggs of both species were present. "Only" refers to stations where that species' eggs were present.

Age		Anchovy			Sardine		
group	Variable	All	Both	Only	All	Both	Only
A1	Mean	62.92	67.49	59.11	19.53	26.58	6.66
	SE	8.70	12.70	11.99	7.01	10.70	2.33
A2	Mean	22.90	36.07	16.32	6.73	12.35	2.16
	SE	3.73	9.34	2.93	1.84	3.91	0.66
B1	Mean	31.05	37.59	26.60	2.14	2.88	0.77
	SE	5.35	7.92	7.25	0.48	0.71	0.33
B2	Mean	9.36	11.15	8.46	1.32	2.62	0.23
	SE	1.31	2.37	1.58	0.57	1.24	0.12

3). Peruvian anchovy egg production was relatively even in all sectors of the inshore region. The mortality rates of both Pacific sardine and Peruvian anchovy were highest in the northern region. Pacific sardine mortality rates were higher than Peruvian anchovy mortality rates in each region.

Mortality rates of Peruvian anchovy and Pacific sardine eggs were not higher where the eggs occurred in the same samples (Table 4). Pacific sardine egg production, in areas where Pacific sardine eggs were not accompanied by Peruvian anchovy eggs in a sample, was only a third of that where the two species' eggs were found together. As in the case of abundance, Peruvian anchovy egg production and mortality rates do not appear to be related to the presence of Pacific sardine eggs in the sample.

The spatial overlap of the Pacific sardine spawning areas and Peruvian anchovy spawning areas cannot be distinguished from randomness. The probability that a 0.05 m^2 sampler will miss a Peruvian anchovy egg patch was 0.47 and for a Pacific sardine egg was 0.61 in August–September of 1981 off northern and central Peru. The joint probability of a sampler of this size missing both species' eggs as estimated from the product of the individual species' probabilities was 0.29. The measured probability of missing both species was 0.28 (Table 1). Therefore based on occurrence in a 0.05 m^2 mouth area sampler, the small-scale spatial distribution of Pacific sardine and Peruvian anchovy eggs was indistinguishable from total independence of each other.

In summary, the results of this study show that Pacific sardines and Peruvian anchovies spawned along the coast over the latitudinal extent of northern and central Peru with the preponderance of spawning within 30 nmi of the coast. The production rate of Peruvian anchovy eggs per unit area (104 eggs/0.05 m^2 d^{-1} was about double that for Pacific sardine (56 eggs/0.05 m^2 d^{-1}) and the mortality rate of Peruvian anchovy eggs ($z = -1.12$ or 67% d^{-1}) was substantially lower than that of Pacific sardine ($z = -2.12$ or 88% d^{-1}). The highest mortality rate for both species occurred in the northern region (IMAR11). For the Pacific sardine in the northern region, the instantaneous rate was -3.88 (98% d^{-1}). For the Peruvian anchovy in the north, the instantaneous rate was -2.14 or 88% d^{-1}. Mortality rates of Peru-

TABLE 3.—Regional egg production (P_0) and mortality rates (Z) of Pacific sardine and Peruvian anchovy as estimated by a nonlinear least squares procedure assuming an exponential model.

Species	Category	Production (SE) eggs/0.05 m^2/d	Mortality (SE) daily instantaneous
Sardine	IMAR11	16.6 (2.6)	3.88 (0.39)
	IMAR21	0.4 (0.1)	1.28 (0.35)
	IMAR31	8.7 (1.5)	1.47 (0.28)
Anchovy	IMAR11	22.0 (9.2)	2.14 (0.83)
	IMAR21	23.7 (6.7)	0.93 (0.36)
	IMAR31	17.0 (4.9)	0.90 (0.35)

TABLE 4.—Egg production (P_0) and mortality rates (Z) of Pacific sardine and Peruvian anchovy for all inshore regions where samples are positive for either species. "All" refers to all stations where eggs of that species were present. "Only" refers to stations which were positive for one species but the eggs of the other species were absent. "Both" refers to stations where eggs of both species were present.

Species	Category	Production (SE) eggs/0.05 m^2/d	Mortality (SE) daily instantaneous
Sardine	All	56.3 (3.2)	2.12 (0.10)
	Only	20.2 (0.4)	2.22 (0.03)
	Both	64.1 (9.2)	1.75 (0.22)
Anchovy	All	104.7 (37.2)	1.12 (0.44)
	Only	109.9 (47.0)	1.35 (0.58)
	Both	104.0 (25.5)	0.90 (0.28)

vian anchovy and Pacific sardine eggs were not higher where the eggs occurred in the same sample.

DISCUSSION

In this section we will discuss Pacific sardine and Peruvian anchovy egg production and mortality off Peru, fundamental statistical problems to be overcome in future studies, some other mechanisms of population control, and egg cannibalism and population control in pelagic spawning, schooling coastal pelagic fishes.

Pacific Sardine and Peruvian Anchovy Egg Production and Mortality

It appears that Pacific sardines and Peruvian anchovies off Peru select the same large-scale sites for egg deposition but select independently of each other at the small scale. While the eggs of both species were concentrated in the inner 30 miles of the survey pattern (Fig. 2), the probability of occurrence on a sample-by-sample basis was not demonstrably different from independent distributions for the two species (Table 1).

Where Pacific sardine and Peruvian anchovy eggs occurred together, Peruvian anchovy egg production rates were equal to those sites where Peruvian anchovy eggs occurred alone, but Pacific sardine egg production rates were higher at co-occurring sites than those sites where only Pacific sardine eggs were taken. Mortality rates where both occurred were marginally lower than where each occurred separately: this implies that the proximity of the adults of the other species does not affect the egg mortality rates. The northern region had the maximum rate of mortality for both Peruvian anchovy and Pacific sardine. The northern region had also the maximum regional rate of production for Pacific sardine, virtually equal to the Peruvian anchovy egg production rates of the other two regions (Table 3).

In all regions, the Pacific sardine mortality rate was higher than the anchovy mortality rate. Of an estimated 2,094 eggs produced/m^2 d^{-1} by Peruvian anchovy, 1,410 (67%) died on the first day. Of an estimated 1,126 eggs produced/m^2 d^{-1} by Pacific sardine, 990 (88%) died on the first day. We suggest two explanations for the cause of higher mortality rate of Pacific sardine eggs relative to Peruvian anchovy eggs in the same region: Moser[4] pointed out that the ovoid shape of the anchovy egg (0.7 × 1.4 mm) as compared with the spherical sardine egg (1.4 mm) may reduce the chance of being eaten by filter-feeders. Author H. Santander has observed that sardine eggs are more delicate to handle in the laboratory. This may mean that the integument of the sardine egg is more susceptible than the anchovy egg to physical damage by predators in the sea. Their susceptibility to damage might also explain their apparent low incidence in juvenile and adult sardine and anchovy stomachs, because broken eggs might not be detected (Santander et al. 1983).

Fundamental Statistical Problems

Errors in the estimation of the slope parameter induce errors of the same sign in the intercept parameter: for this reason there are major problems in comparing adult spawning biomass concentration derived from the intercept parameter and egg mortality rate derived from the slope parameter. Thus, for the purpose of this paper, the comparison of spawning biomass concentration and egg mortality is not reported as a result of this research. Instead, Figure 3 and Table 6 are points of discussion. The data come from a plan for stock assessment and as such are not definitive on the question of biomass concentration and egg mortality rate. The relationship is suggestive, however, and may be used to design a study of cannibalism that is not statistically confounded.

The statistical problem of patchiness (Taft 1960), encountered when estimating the abundance of fish eggs, becomes more severe when estimating production and mortality of eggs because the intensity of patchiness changes with age (Smith 1973, 1981; Smith and Hewitt 1985a, 1985b; McGurk 1987). Since the mortality estimate requires the arithmetic means (Southwood 1978), log transformation to stabilize variance is not used.

Egg production (P_0) and mortality rate (Z) are determined using the exponential mortality model (Picquelle and Stauffer 1985). It has been determined that the midpoint of spawning is at 2200 hours but samples from the spawning interval are biased (Smith and Hewitt 1985a). The intercept and mortality rate could be systematically underestimated if the actual mortality rate

[4]H. G. Moser, Southwest Fisheries Center La Jolla Laboratory, Natl. Mar. Fish. Serv., La Jolla, CA 92038, pers. commun. May 1983.

in the initial period was higher owing to an interaction between local density and mortality rate on eggs at the highest distributional densities (McGurk 1987).

The Central Limit Theorem requires independence among sample values. With the spawning of Pacific sardine and Peruvian anchovy off Peru compressed against the coast in a 30 mile band in 1981, abundance estimates from stations separated in the cross-shelf dimension at 3 mile intervals are not likely to be independent. The effect will be an underestimate of sample standard error of the mean (Table 2). The degree of the same type of error in the along-shelf plane was probably smaller because the transects are 10 nmi apart. Also the collection of sites used for the estimates of abundance of 1 and 2 d old eggs in the first half of each day (A1 and B1 in Table 2) are from different stations from those used for estimates of abundance of 1 and 2 d old eggs in the second half of each day (A2 and B2 in Table 2).

Other Mechanisms

Egg cannibalism is probably only one of several possible population controlling mechanisms in anchovies. For example, cannibalism could occur at life stages other than the egg stage. There have been recent observations, in the laboratory, of older anchovy larvae consuming younger larvae (Brownell 1985). In these observations, the larvae became more vulnerable as pigmentation formed in their eyes and integument.

Energy demands for egg production and spawning could lead to aggregations of adults where food production and, coincidentally, egg mortality are both high. That, in both Pacific sardine and Peruvian anchovy, higher rates of egg mortality and egg production occurred in the same region (IMAR11) seems to support this view. Lastly, from laboratory observations, northern anchovy larvae, only a day old, may seek and maintain position in patches of *Gymnodinium*, making these larvae vulnerable to enhanced feeding activity by many other organisms in the same patch or layer (Hunter and Thomas 1974).

Egg Cannibalism and Population Control

For the northern anchovy, *Engraulis mordax*, Peterman et al. (1988) concluded that the size of the recruited stock is not determined in the first 20 days following spawning. On the other hand, Pauly[5] concluded that egg mortality due to cannibalism by the adult stock is a primary density dependent control on recruitment in the Peruvian anchovy, *Engraulis ringens*. Smith (1985) lists three situations in which cannibalism by schooling pelagic spawners would be an effective population controlling activity: 1) directed filtering behavior on dense aggregations of eggs; 2) encounter with other schools' patches of eggs; and, 3) anchovy population switching from biting to filtering behavior.

Directed Filtering

In the first few hours after spawning, before much dispersal has taken place, directed filtering could be an important source of mortality (Smith and Hewitt 1985b; McGurk 1987). Hunter and Dorr (1982) found that adult northern anchovy filtering was induced by 5 northern anchovy eggs/L and sustained by 1 or 2 eggs/L in laboratory tanks. Given that the level of artificial feeding is higher for laboratory animals and that probably the quality of water for sensing prey is lower, these thresholds may be higher in the laboratory than in the sea. One disadvantage of this mechanism for population size control is that, because of proximity, the most likely school to encounter the newly spawned patch is the school from which the spawn was produced. Santander et al. (1983) found that Peruvian anchovy eggs < 2 hours old were overrepresented by a factor of three in the stomachs of Peruvian anchovy relative to their incidence in the sea. In a typical spawning school (Santander et al. 1984; Alheit 1985), there would be 10 times as many Peruvian anchovies feeding on eggs than females spawning eggs. While the mortality rate might be sufficient, it is difficult to seen how a change, in population size or in density over thousands of square kilometers, could materially affect a species grazing for a few hours on its own eggs over a range of a few hundred meters. This source of mortality, although large, may not be sufficiently variable with population density to control recruitment.

[5]The estimate of instananeous mortality "z" derived by Pauly (1987) is strongly biased downward at low mortality rates but should still be valid at high levels of parent stock. Daniel Pauly, International Center for Living Aquatic Resources Management, Manila, Philippines, pers. commun. March 1989.

Encounter

Incidental filtering of eggs by encounter of other schools' patches of eggs would appear to be a direct mechanism for parental control of recruitment rate and population density. If one combines the information on egg cannibalism rate by Alheit (1987) and the demographic influence on population annual fecundity reported by Pauly and Soriano (1987) (Table 5), one can see that the effective fecundity (eggs hatched after cannibalism) would be low when the stock was composed primarily of juveniles and first-year spawners.

TABLE 5.—Age-specific rates of cannibalism and egg production for anchovy.

Age (yr)	Anchovy egg production[1] (eggs/g/d)	Anchovy egg consumption[2] (eggs/g/d)	Effective fecundity (eggs/g/d)
Juveniles[3]	0.	9.3	−9.3
1	3.9	9.3	−5.4
2	9.0	9.3	−0.3
3	15.7	9.3	6.4
4	18.4	9.3	9.0

[1]Pauly and Soriano 1987
[2]Alheit 1987
[3]Ciechomski 1967

Switching

It is also possible for cannibalism to interact indirectly with population density. An indirect method for population control is evident if one considers a system where the anchovy prefer to feed by biting relatively large zooplankton and where filtering occurs only when large zooplankton are low in abundance (O'Connell 1972). Under these circumstances predation by anchovy on the major herbivores could result in a larger standing crop of phytoplankton and in increased rates of anchovy filtering (MacCall 1980). In the course of switching to a preponderance of feeding by filtering, the anchovy would inadvertently filter anchovy eggs at a higher rate.

Egg production rate was sixfold higher in Peruvian anchovy compared with northern anchovy off California (Smith and Hewitt 1985a). Of the 2,094 Peruvian anchovy eggs produced per square meter, 67% died on the first day while off California; of the 300 northern anchovy eggs produced per m^2, 22% died on the first day. While anchovy are omnivorous in both areas, phytophagy is considered more pronounced off Peru (MacCall 1980).

Pauly (1987) found that knowledge of the rate of cannibalism appears crucial for managing the Peruvian anchovy. The rate of cannibalism on eggs is admittedly high, but it may be that the variation in the rate of cannibalism is insufficient to explain the variation in the rates of recruitment. It remains to be seen if interannual differences in the relative proportion of feeding by filtration on the one hand and biting on the other hand are sufficient to explain differences in recruitment.

The difference in conclusions regarding northern anchovy egg cannibalism between Peterman et al. (1988) for California anchovy and Pauly (1987) for the Peruvian anchovy, may be due to a simple difference in population density between the two regions, California having a much lower population density than Peru. Pauly (1987) showed the relationship between population size and egg mortality: a better relationship would be between local population density and egg mortality (Csirke 1980; MacCall 1980; Ware and Tsukayama 1981).

Egg mortality rate and adult biomass density are closely related in interregional and interannual egg production assessments (Fig. 3). The relationship is surprisingly close when one considers biomass of juvenile anchovy, the biomass of other filtering fishes, particularly sardines, and the biomass of invertebrate predators have been neglected. In Table 6, one can see that northern anchovy assessment studies off California (Stauffer and Picquelle 1981; Stauffer and Charter 1982; Picquelle and Hewitt 1983, 1984; Hewitt 1985; Bindman 1986) and South Africa (Armstrong et al. 1988) differ a great deal from the assessment study reported in this paper for Peru. The median biomass density of adult anchovy was 6 g/m^2 off California between 1980 and 1985, while the median percent eggs dying each day was 16%/d. In the south Benguela Current, the mean biomass density of adult anchovy was 12 g/m^2, and the mean percentage of eggs dying per day was 22% (Armstrong et al. 1988). The median regional estimate for 1981 of biomass density of adult anchovy was 33 g/m^2 off Peru, and the egg mortality was 61% egg mortality per day. While these observations suggest cannibalism as a cause, the mortality rate of eggs may only be a consequence of generally higher populations of a wide range of other vertebrate and invertebrate predators in prime schooling fish-feeding areas.

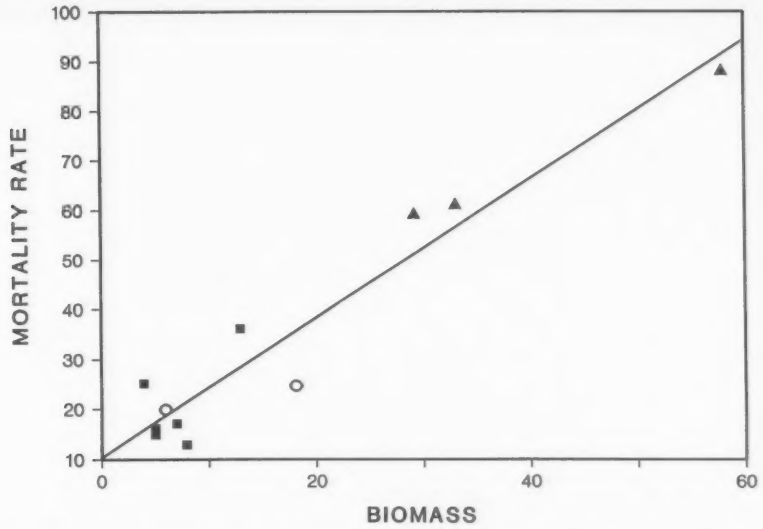

FIGURE 3.—Mortality rates in percent per day of anchovy aggs as a function of anchovy spawning biomass concentration in grams per square meter; closed triangles, Peru in nearshore regions IMAR11, IMAR21, IMAR31 (this paper); closed squares, values for the entire spawning region off California from 1980 to 1985 (Stauffer and Picquelle 1981; Stauffer and Charter 1982; Picquelle and Hewitt 1983, 1984; Hewitt 1985; Bindman 1986); and, open circles, for the entire spawning region off South Africa in 1985 and 1986 (Armstrong et. al. 1988).

TABLE 6.—Anchovy egg mortality rate and adult spawning biomass concentration in the Humboldt (*Engraulis ringens*), California (*E. mordax*), and southern Benguela (*E. capensis*) currents.

Year/region	Spawning area (km^2 $\times 10^{-3}$)	Spawning biomass (tons $\times 10^{-3}$)	Biomass concentration $g\ m^{-2}$	Egg mortality $\%\ d^{-1}$
Peru 8108				
IMAR11	7.9	460	58	88
IMAR21	12.9	420	33	61
IMAR31	11.2	320	29	59
CalCOFI 8003[1]	66.1	870	13	36
CalCOFI 8102[2]	77.5	635	8	13
CalCOFI 8202[3]	83.0	415	5	15
CalCOFI 8302[4]	94.7	652	7	17
CalCOFI 8402[5]	61.6	309	5	16
CalCOFI 8502[6]	132.2	522	4	25
Benguela				
1985[7]	107.1	614	6	20
1986[7]	109.8	2006	18	24

[1]Stauffer and Picquelle 1981.
[2]Stauffer and Charter 1982.
[3]Picquelle and Hewitt 1983.
[4]Picquelle and Hewitt 1984.
[5]Hewitt 1985.
[6]Bindman 1986.
[7]Armstrong et al. 1988.

CONCLUSION

MacCall (1980) stated that only 10% of the apparent control of northern anchovy recruitment off California may be due to stock size, with the vast majority of control arising from means that are independent of stock size. Lasker and MacCall (1983) concluded that the best measures of the stock recruitment curve are not sufficient domed for cannibalism to be a "major regulatory mechanism". Also, it appears from examination of the life stages of northern anchovy (Smith 1985, table 3) moderate reproductive failures could happen at the fecundity, embryonic, larval, and juvenile prerecruit stages, but a reproductive success of great proportions would most likely arise at the embryonic and larval stages. The size of the recruited year class will accumulate the rates of early stages, and the later the prerecruits are evaluated, the more likely the reproductive success will have been established. Peterman et al. (1988) evaluated only the first 20 days of life.

For 6 successive years (included in Peterman et al. (1988)), the interannual coefficient of variation of the spawning biomass was 35% and the interannual coefficient of variation of recruit-

ment was 104%. Only two life history parameters varied more than the spawning biomass (35%): adult density per unit area (47%) and egg mortality (38%) (Smith and Moser 1988). While cannibalism is sufficiently important as a source of egg mortality to control the size of populations like sardine and anchovy over the long term, it is unlikely that the interannual variation in rates of mortality due to cannibalism are sufficient to cause major recruitment variations. One would suspect that variability in egg mortality rate could arise from the 70% of egg mortality not due to cannibalism. Off California, Theilacker (1988) has estimated that the rate of northern anchovy egg consumption by juvenile and adult euphausiids may account for 28% of the egg mortality. Other influences on recruitment could arise from copepod predation on yolk-sac larvae (Lillellund and Lasker 1971) and predation of Pacific mackerel on juveniles (Methot 1986[6]).

To manage variable stocks like the sardine and anchovy it may be sufficient to monitor the age structure of the catch and the production and survival of the embryonic stage (Methot and Lo 1987[7]). A decrease in the number of older, highly fecund, spawning age classes will decrease effective population fecundity. In filter feeders like sardine and anchovy, cannibalism by younger age classes may lower the survival of eggs. Thus, merely by monitoring age structure and egg survival one can project when large, unusually successful year classes are possible. New techniques for monitoring juvenile abundance and growth will be required when a sardine or anchovy fishery becomes so intensive that an early recruitment prediction is necessary.

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Ageing and Back-Calculating Growth Rates of Pacific Herring, *Clupea pallasii*, Larvae by Reading Daily Otolith Increments

Erlend Moksness and Vidar Wespestad

ABSTRACT: Newly hatched Pacific herring, *Clupea pallasii*, from eastern Bering Sea were released into an outdoor concrete basin and raised on natural plankton. The larvae were sampled frequently during the first two months, and a growth curve for that period was established. Otoliths from 52 herring larvae, collected over the entire experimental period, were examined for daily increments. Increments were formed on a daily basis from the end of the yolk-sac stage (age 8 days) and were found to be independent of the growth rate of the herring larvae. The increment widths, however, reflected the growth rate of the larvae.

Otoliths have been used to estimate daily age and growth since Pannella (1971) reported that the number of primary increments in otoliths approximated daily deposition. Brothers et al. (1976) raised northern anchovy, *Engraulis mordax*, and California grunion, *Leuresthes tenuis*, from eggs in the laboratory and verified that increment formation occurred daily. Jones (1986) found that daily increment analysis had been applied to at least 29 species of larval fish to estimate age, but validation of the technique was based on laboratory observations that may be invalid for wild populations. Atlantic herring, *Clupea harengus*, have been investigated for daily increment formation (Gjøsaeter and Øiestad 1981; Geffen 1982; Lough et al. 1982; Jones 1985; Messieh et al. 1987). Contradictory findings by various authors have created controversy concerning whether Atlantic herring deposit growth increments on a daily basis. Gjøsaeter and Øiestad (1981) found 99 increments in 97 d herring grown in a large outdoor enclosure; however, their sample size was too small to be conclusive (Jones 1986).

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The early life history of Pacific herring, *Clupea pallasii*, from the eastern Bering Sea was studied in the same enclosure as Gjøsaeter and Øiestad's (1981). All the herring were spawned on the same day, and larvae hatched over a 3 d period. Otoliths were examined periodically during the experiment and from surviving individuals at the termination of the experiment.

MATERIAL AND METHODS

Pacific herring eggs were collected from the spawning grounds in Bristol Bay, AK at low tide on 24 May 1986. The eggs collected had been deposited between 22 May and 23 May on intertidal rockweed, *Fucus* sp. Water temperature at the time of spawning was 4.5°C and salinity was 30‰. Further spawning did not occur (before or after) in the area in which the eggs were collected. *Fucus* fronds with light egg coverage (1–2 egg layers) were collected at random within the spawning area, packed into half liter plastic bags, filled with seawater, and sealed. A total of 25 bags were filled with about 2,000 eggs/bag. The bags were placed in insulated shipping containers with gel ice, which were shipped via air to the Flødevigen Biological Station in Arendal, Norway. Upon arrival at Flødevigen the eggs were unpacked and placed in hatching boxes, which were supplied with flowing seawater at 7.7°C and at salinity of 32‰.

The eggs began hatching on 10 June 1986 and finished by 12 June 1986. Fifty percent hatching (11 June) was defined as day 0 (age = 0) in the experiment. Newly hatched larvae were collected from incubation boxes in white plastic cups in groups of 5–25, counted, and transferred to 5 L cylinders, which were placed in an 8.1°C water bath. A total of 25,200 larvae hatched from an estimated total of 50,000. The eggs were not treated during incubation and a heavy fungus growth developed. This caused most of the egg mortality.

On 13 June (age 2 days) 24,840 larvae were released into a large artificial outdoor basin—2,000 m^3 in volume, 600 m^2 in surface area, and 3.5 m at maximum depth. The basin had been filled with seawater pumped from a depth of 19 m. At the time the larvae were introduced, phytoplankton and zooplankton production was high. The basin was drained on 12 August, and the remaining herring larvae in the basin were collected (age = 62 days).

The larvae in the basin were sampled daily using a two-chambered plankton net of 500 μm mesh and a total sampling area of 0.3 m^2. The net was drawn diagonally across the basin at a depth of 2 m and the total volume sampled was 7.5 m^3. All the sampled larvae were preserved in 80% buffered ethanol. A more detailed description of the basin experiment is given in Wespestad and Moksness (1989)[1]. The standard length (snout to the tip of the notochord or hyplural plate) of the larvae/juveniles were measured to the nearest 1.0 mm. The largest otoliths, the sagittae, were removed and mounted on a glass plate with clear nail polish. The dry weight of each individual was measured to the nearest ±1 μg, after drying at 60°C for 24 hours. Otoliths of herring juveniles over 30 mm had to be ground, to expose growth rings. This was done with fine grit paper (30 μm and then 0.3 μm). The maximum magnification that could be used to read the growth rings in the microscope was × 400, owing to insufficient light penetrating the section. Table 1 gives an overview of the number of larvae used in otolith analyses. A detailed description of the otolith analyzing system and the method used are given in Andersen and Moksness (1988).

TABLE 1.—The number of larvae examined for daily increments by date.

Date	Age	Number examined
25 June	14	1
3 July	22	2
10 July	29	5
14 July	33	5
18 July	37	5
21 July	40	5
27 July	46	10
12 Aug.	62	19

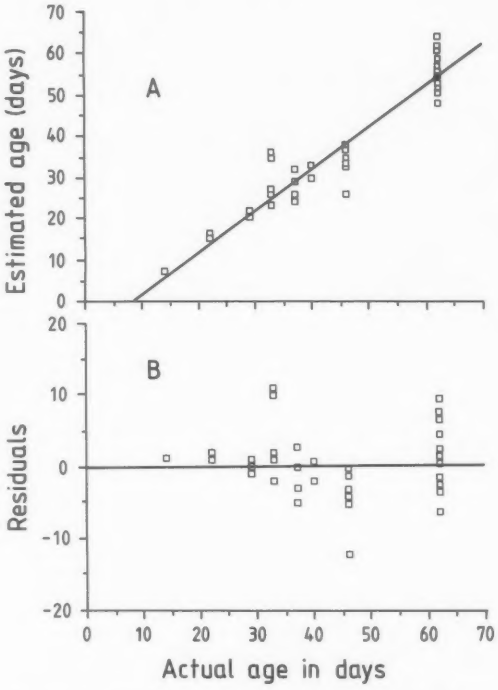

FIGURE 1.—Relationship between estimated and actual age of Pacific herring in days (A), $y = -8.3 + 1.0144\,x$, $r = 0.96$; and the pattern of the residuals (B).

RESULTS

The relationship between the estimated age (estimated number of rings) and the actual age of the herring larvae is shown in Figure 1. The residuals are shown in the same figure. The relationship was linear, and the deposition rate was not significantly different from one increment per day from age 8 days of the larvae (t-test; t = 0.08, df = 50). The residuals were equally distributed around zero indicating no trend in the data. The discrepancy did not tend to change sign or range with the age of the larvae (Fig. 2), indicating that the frequency of daily increments in the otoliths did not change with the age of the larvae. The standard deviation of estimated age from real age was ±4.2 days with a range from −12 to +11 days; therefore, there is little correlation between estimated age and length (Fig. 3). Apparently, there is no relationship between the rate of otolith ring deposition and larval growth.

All three relationships between larval standard length and otolith radius exhibited a good fit to the data (Fig. 4, $r > 0.96$), but the first, the

[1]Wespestad, V., and E. Moksness. 1989. Observations on the growth and survival during the early life history of Pacific herring, *Clupea pallasi*, from Bristol Bay, Alaska, in a marine mesocosm. Submitted Fish. Bull., U.S.

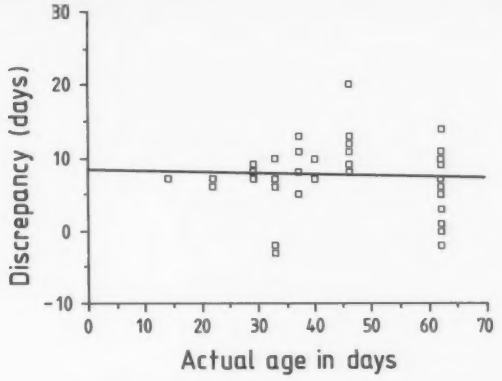

FIGURE 2.—Discrepancy between estimated age (real age minus estimated age) and actual age of Pacific herring as a function of actual age. $y = 8.3 - 0.014\,x$, $r = 0.05$.

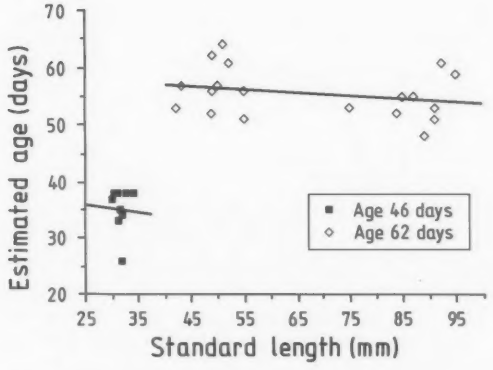

FIGURE 3.—Relationship between estimated age and standard length in Pacific herring larvae of same age. Age 46 days: $y = 39.63 - 0.14\,x$, $r = 0.04$; age 62 days: $y = 59.53 - 0.06\,x$, $r = 0.27$.

fourth order polynomial, provided the best fit to the initial length of the larvae.

The average daily growth rate (±1 SD) calculated from all otoliths with the fourth order polynomial is presented in Figure 5 along with the estimated minimum, maximum, and average growth rate obtained from the herring measured at termination of the experiment. The relationship shows that there is a high similarity in the trends of the growth curves between the different age groups. The daily growth rate calculated from the standard length of the larvae at termination of the experiment showed an average of 0.66 mm/d, a minimum of 0.31 mm/d, and a maximum of 1.48 mm/d. Estimation of the average growth rate, using these data, gives an average growth rate of 0.73 mm/d.

DISCUSSION

The results of this study show evidence of daily increments in the otoliths of Pacific herring, agreeing with earlier investigations on the same species (McGurk 1984a). A difference of eight days was observed between the estimated

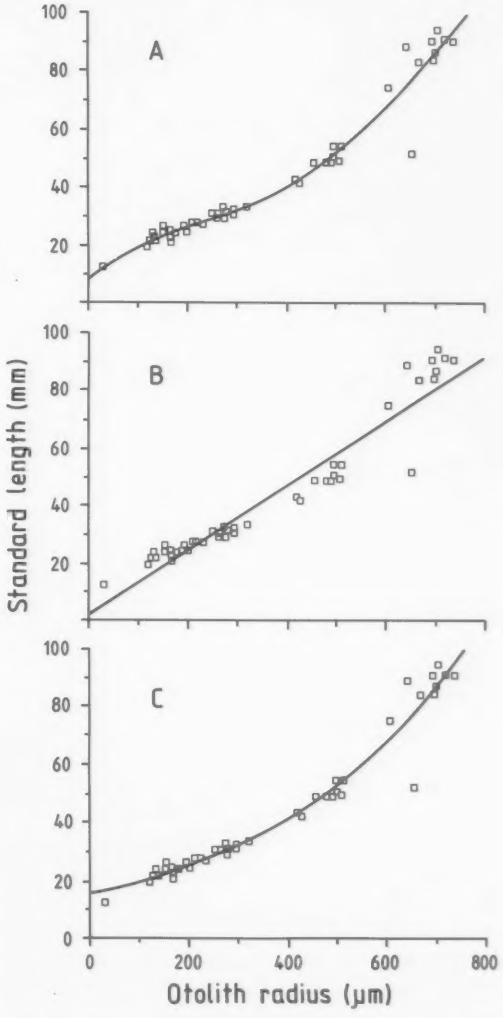

FIGURE 4.—Relationship between otolith radius (x) and standard length (y) of the Pacific herring larvae. A: $y = 8.1461 + 0.1542\,x - 4.875 * 10^{-4}\,x^2 + 9.651 * 10^{-7}\,x^3 - 5.038 * 10^{-10}\,x^4$, $r = 0.98$. B: $y = 2.6738 + 0.1123\,x$, $r = 0.96$. C: $y = 15.6952 * 10^{(0.0011\,x)}$, $r = 0.98$.

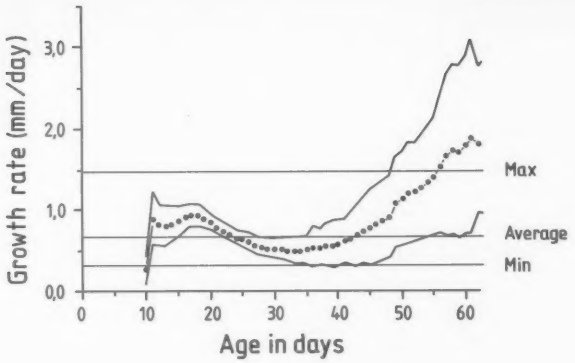

FIGURE 5.—The average daily growth rate (mm/day) estimated from otolith analyses (·) with ±1 SD. The minimum (min), average, and maximum (max) growth rate (mm/day) calculated from Pacific herring surviving to the termination of the experiment (day 62) are indicated.

and the actual age of the larvae; this difference corresponds well with the end of yolk-sac stage of the same larvae (Wespestad and Moksness fn. 1); it is three days later than that found by McGurk (1984b) for Pacific herring larvae at the same temperature (8.0°C).

The results are the same as earlier investigations on Norwegian spring spawning herring in a 4,400 m^3 outdoor basin (Gjøsaeter and Øiestad 1981) in which herring form one otolith increment per day. However, the results of one increment per day contradicts findings from laboratory experiments in which otolith increments were not formed daily. Geffen (1982) on Atlantic herring and McGurk (1984a) on Pacific herring found the growth rate of the larvae and the number of increments in the otoliths to be correlated, while our results show a poor correlation between growth and daily increments. The expected standard deviation was ±1 day, based on the observed range in hatching time; however, the estimated variation was much greater than this. A possible explanation for this discrepancy might be that the minimum growth rate (0.31 mm/d) observed in this study was greater than growth rates observed in laboratory studies.

Geffen (1982) reported that growth coefficient tended to increase with the increase in size of aquarium used—from the 120 L laboratory tanks up to 4,000 m^3 mesocosms. The difference in data between experiments using small and experiments using large rearing tanks results from an inability of larvae to form daily increments at low growth rates (Moksness et al. 1987). In our work, the average growth rate corresponded to the growth rate observed in nature. Checkley (1982)[2] reported otolith increments and fish length for juvenile herring captured in Bristol Bay in autumn 1981. From these data, we estimated the average daily growth rate over the first summer of life to be 0.74 mm/d, which is similar to the average growth rate observed in this experiment. Therefore, it appears that conditions in the basin were similar to the average conditions larvae experience in its natural habitat.

Otolith increment size was well correlated with the measured growth in standard length of the larvae. The preferred growth model (see Figure 4a), gave a good fit to the observed values, however small the sample size and especially for the smallest larvae, but the growth model did not rule out the applicability of other models. An exponential model might fit better with more available data. When fitting the data on dry weight of the larvae to the radius of the otolith, a very good fit was observed for the exponential equation.

The resulting daily length increment from the fourth order polynomial growth model approximated the calculated daily length increment based on observed length-at-age reported by Wespestad and Moksness (fn. 1). By estimating the relationship between the standard length of the larvae and the radius of the otolith, the daily length-increment of the fish could be described.

[2]Checkley, D. M. 1982. The ageing of juvenile Pacific herring by otolith analysis. Final Report, NOAA contract 82-ABA-1001. Northwest and Alaska Fisheries Center.

The range in the residuals and deviations reported in this paper are believed to be, in part, due to the use of × 400 magnification. This has been shown to be too low to give good resolution of the otoliths (Campana et al. 1987).

Three general conclusions can be drawn from this study: 1) Daily otolith increments in Pacific herring larvae are true daily increments at normal rates of growth. 2) The results, showing poor correlation between length and age, suggest that age in days can be estimated only from direct ageing and that attempts to establish age from age-length relationships may produce significant errors. These types of error may be important in stock separation studies such as distinguishing between spring and autumn spawned herring (Fossum and Moksness 1988). 3) Mesocosms may be a more appropriate environment for studying marine fish larvae and juveniles than laboratory-sized rearing tanks. Growth appears to be influenced by container size. Mesocosms have been shown to produce growth rates for other species such as capelin, *Mallotus villosus*, similar to that observed in the field (Gjøsaeter and Monstad 1985).

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Egg Size, Female Effects, and the Correlations Between Early Life History Traits of Capelin, *Mallotus villosus*: An Appraisal at the Individual Level[1]

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ABSTRACT: The authors examined the within-individual correlations between egg quality (quantified by yolk volume) and early life history traits in capelin, *Mallotus villosus*. The commonly reported generalization—large eggs produce large larvae that subsist longer on endogenous energy reserves—was not supported by our analysis. Post-hatching lifespan of unfed larvae did not vary with initial egg yolk volume, yolk-sac volume at hatching, or size at hatching. The only correlate of post-hatching lifespan was a direct relationship with oil globule volume at hatching. Size and age at hatching covaried directly, but hatching later exacted a cost on yolk reserves. Significant female influences on these early life history traits of offspring were found. Initial egg yolk volume and oil globule volume at hatching contributed most to the rejection of the null hypothesis of no female effect. None of the early life history traits examined was correlated with female size, but female condition and lipid indices were directly correlated with average initial yolk volume.

Most individuals in marine fish populations die before feeding begins (Hewitt et al. 1985; Ware and Lambert 1985; McGurk 1986; Taggart and Leggett 1987a). Central to much of Reubin Lasker's work was the role of timing in survival during these early life stages. This was explicit in his early papers on temperature-dependent developmental rates (Lasker 1962, 1964; Zweifel and Lasker 1976) and became an implicit part of his "stable oceans hypothesis" (Lasker 1975, 1981, 1985), which postulates that coincidence in the timing of physical oceanographic conditions favoring food production and the timing of first feeding in fish larvae is critical to larval survival. Peterman and Bradford (1987) recently evaluated interannual variability in both the frequency of turbulence-generating winds and the survival of northern anchovy, *Engraulis mordax*, larvae and found an inverse relationship between these two events.

Temporal matching of resources and consumers is one of degree as timing of early life history (ELH) events varies even under constant conditions (Chambers and Leggett 1987, 1989; Chambers et al. 1988). Knowledge of the within-population variation in ELH traits is, therefore, crucial for estimating the number of larvae that establish feeding, and thus retain the potential for recruitment to the fishery. To Lasker's credit, his temperature-dependent development experiments in sardines, *Sardinops sagax*, were conducted on individual embryos isolated in incubation chambers in order "to assess their individual variability of development and growth" (Lasker 1964, p. 399). While variability in hatching age within and across temperatures is apparent from Lasker's plot of age at hatching of individual sardines versus temperature, the potential relevance of this variability to survival was not discussed further.

Variable provisioning of energy reserves to embryos is one of several mechanisms that could generate variability in size at hatching, in size and age at first feeding, in ability to withstand starvation, and, consequently, in survival to and during the critical switch from endogenous to exogenous nutrition. It is often reported that larger eggs produce larger larvae that subsist longer without food (e.g., Blaxter and Hempel 1963). Although this has become doctrine in reviews of marine fish early life histories (Blaxter 1969, 1988; Hempel 1979; Hunter 1981; Rothschild 1986), at least one of three caveats applies to work that has led to this generalization. 1) Eggs were grouped either by size (e.g., small vs.

[1]Contributions to the programs of GIROQ (Groupe interuniversitaire de recherches oceanographiques de Quebec) and the Huntsman Marine Science Centre.

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large) or source (e.g., full-sibling groups) and the analysis of the influence of egg size on ELH traits was conducted among these groups. Correlations, when reported, were based on the average trait values in these groups. Such analyses obscure variation in and correlation between traits at the individual level—where natural selection acts. 2) Simple correlations were calculated. These may reflect the response of two traits to a third covarying trait rather than appraise the influence implied. 3) Egg size was confounded with other factors not explicitly considered (e.g., different source populations, seasons of spawning, years, and ages of females). The influence attributed to egg size is, therefore, equivocal. These are important limitations. The estimates of relationships between egg size and subsequent ELH traits so derived cannot be presumed to be of the same magnitude or statistical significance as those from within-individual observations. The conclusions of previous studies must be viewed as provisional demonstrations of associations of egg size with the ELH traits considered.

The extent to which relationships exist at the individual level between egg size, hatchling size, and prestarvation lifespan remains unanswered. In this paper we analyze such ELH trait covariation in capelin, *Mallotus villosus*. We address two questions: First, which pairs of ELH traits covary when evaluated at the individual level while (statistically) holding other traits constant? Of particular interest is which, if any, of these traits vary with egg quality. Second, is the pattern of ELH trait variation attributable to maternal influences?

METHODS

Spawning capelin were collected on 23 and 25 June 1988 at spawning sites in eastern Newfoundland, Canada (lat. 49°39′N, long. 52°41′W). These capelin were held in a 1,000 L flow-through tank at the Marine Science Research Laboratory, Logy Bay, Nfld. until 28 June when crosses were performed. Eggs from each of 10 females were fertilized with milt from one male. This provided a range of eggs sizes and created the potential for female effects on ELH traits of offspring while minimizing male influence.

Yolk diameters of 12–15 eggs per female were measured at 20–28 h postfertilization at a magnification of 40×. These embryos were in the blastula stage and their yolks remained approximately spherical. Embryos were then transferred individually to separate wells of 12-well tissue culture plates. These plates served to limit possible interaction among incubating embryos (e.g., bacterial growth on dead eggs) by keeping embryos at least 3.5 cm apart. In total, 142 eggs were housed in 12 plates, each containing 1 or 2 fertilized eggs per female. Each set of 4 plates was submerged to a depth of 10 cm in a separate plastic tank containing static seawater; thus, all embryos in a tank were exposed to the same seawater. This seawater was filtered to 1 μm, sterilized with ultraviolet light, and changed every 2 days to ensure sufficient levels of oxygen for the developing embryos. All three static seawater tanks were placed in a common water table maintained at 9.5 ± 0.49°C (mean ± SD). At the late eyed stage, embryos were transferred individually to separate 125 mL glass jars containing 100 mL of filtered, sterilized seawater. Embryos in jars occupied the same location in the water table as they had before transfer. Fluorescent lamps in the laboratory were set to 18 h light, 6 h dark.

Embryos were inspected daily and their day of hatching recorded. Hatchlings were anaesthetized (MS-222, 25 mg/L), measured, revived, and returned to their jars. Total length (TL), length and height of yolk, and diameter of oil globule were measured. Larvae were inspected daily until their death, which was inferred if a larva did not respond to gentle tapping of its holding jar. Deformed hatchlings (3.5%) and those failing to escape the egg membrane (1.4%) were excluded from analyses.

Immediately after spawning, each female was measured (standard length, SL) and frozen. Subsequently, but within 2 months, females were thawed and somatic weights determined. Constant dry weights were achieved after oven drying at 60°C for 48 hours. These dried carcasses were ground and their lipids were extracted by flooding with diethyl ether and decanting (Dobush et al. 1985). Constant lean, dry weights were obtained after three cycles of lipid extraction. Indices of somatic condition (wet weight/SL) and lipid condition (extractable lipid weight/lean dry weight) were calculated for each female.

We analyzed six ELH traits: initial yolk volume (Y1), total length at hatching (TL), yolk volume at hatching (Y2), oil globule volume at hatching (G), age at hatching (H), and posthatching lifespan (L). Initial egg yolk and oil globule at hatching were approximately spherical and we estimated their volumes from their diameters.

Yolk at hatching was approximately a prolate spheroid and we estimated this volume from measurements of length and height of the yolk complement minus the volume of the oil globule it contained.

We used initial yolk volume rather than initial egg volume to quantify egg quality because it better represents the energy content of the egg. We chose posthatching lifespan over the more frequently used time to yolk-sac depletion or time to irreversible starvation ("point-of-no-return", Blaxter and Hempel (1963)), because the latter are much more difficult to determine accurately. We assumed a high correlation between these components of posthatching lifespan for unfed larvae. In support of this assumption we calculated a correlation of $r = 0.88$ ($P < 0.001$) between the interval from hatching to yolk-sac depletion and the interval from yolk-sac depletion to irreversible starvation, using data from 25 marine fish species presented by McGurk (1984).

We accounted for the potential influence of environmental (laboratory) variation on ELH measurements by using location of the embryos and larvae in the water table as a blocking variable. In addition, jars were inspected for hatchlings, and hatchlings were measured, in sequence by block. Block specification thus represented chance differences among the three static tanks; locational differences (which might include effects of slight temperature or light gradients on any of the ELH traits); and effects of unavoidable delays in measuring hatchlings. These delays were caused by the time required to measure the hatchlings. As an extreme example, 30 hours were required to measure all larvae hatching on the modal hatching day.

We employed a two-way randomized block experimental design with female parent as the treatment of interest (i.e., are there significant differences among females in the ELH traits of their offspring?). This design allowed us to determine both the female effect on ELH traits and the within-individual correlations between those traits. The design was unbalanced because the number of eggs used varied (12–15 per female) and some mortality occurred before hatching.

We treated the six traits as a multivariate response and analyzed these as a random-effects multivariate analysis of variance (MANOVA) with the general linear model

$$(Y1, TL, Y2, G, H, L) = \mu + \text{female} + \text{block} + \text{female} \times \text{block} + \epsilon.$$

The six ELH traits of the response vector are defined above, μ is the overall mean, *female* codes for females 1–10, *block* codes for tank/location/monitoring order 1–3, and ϵ is random error from the model.

We calculated partial correlations between all pairs of traits from residuals remaining after the effects of block and the remaining four traits (considered for this procedure as covariables) had been statistically removed. We also calculated simple correlations between all pairs of traits based on average group values (common female parent), as has been the practice in previous work. These correlations were compared with the partial correlations to assess differences in estimated correlations based on the two approaches.

We evaluated the female effect on the trait vector with Wilk's lambda criterion (Timm 1975). After rejecting the null hypothesis of no female effect we gauged the contribution of each trait to this result. This was done by examining the magnitude and sign of the correlation between each trait mean and the standardized and adjusted discriminant function that maximized among-female differences (Timm 1975; Wilkinson 1975). We also compared the MANOVA findings with standard *F*-tests and with percentage of the total variance due to female source as calculated from univariate ANOVA's on each ELH trait. We assessed the influence of female condition on the ELH traits of her offspring by estimating the simple correlation between each family-average ELH trait and female size, condition index, and lipid index.

Prior to analysis we log transformed initial yolk volumes and yolk and oil globule volumes at hatching. MANOVA, discriminant analysis, and partial correlations were performed on SYSTAT (Wilkinson 1988) and the variance components were estimated using SAS (SAS Institute, Inc. 1987).

RESULTS

Survival to hatch was over 98%. The quantity of variation in initial yolk volume, age at hatching, and age at death (C.V. (= SD/mean) = 0.15, 0.03, and 0.24, respectively) was comparable to values reported for other species (cf. Chambers et al. 1988). Length, yolk, and oil globule volume at hatching were more variable than expected (C.V. = 0.08, 0.98, and 1.44) owing partly to their rapid change during the 1–2 days after hatching when measurements were taken. By

measuring larvae in block sequence we reduced this variance due to ontogeny in our analyses of correlations and female effects.

Correlations Between ELH Traits

There were seven significant partial correlations between the ELH traits (Fig. 1). These correlations measure whether or not a change in one trait is associated with a change in the other while holding the remaining (four) traits constant. Size, yolk reserves, and age at hatching all covaried directly with initial yolk volume. Hatchling size increased with age at hatching, but yolk reserves at hatching were negatively related to age at hatching. Yolk and oil globule volume at hatching covaried directly. Oil globule volume at hatching was the only trait that covaried with posthatching lifespan; all else equal, larvae with larger oil globules lived longer.

It is important to note the trait pairs that failed to show associations. Oil globule volume at hatching did not vary with initial yolk volume. Length at hatching was independent of yolk or oil globule volume at hatching. Futhermore, posthatching lifespan was not related to initial yolk volume, length, age, nor yolk volume at hatching.

The correlations between ELH traits based on family averages differed from the partial correlations calculated within individuals (Table 1). The sample size of family groups was small (n = 10), hence, caution is required when assessing the pattern that emerged. First, there were no neg-

TABLE 1.—Simple correlations between early life history traits of capelin, *Mallotus villosus*, calculated from family averages (df = 8). *P<0.05, **P<0.01.

Trait	(1)	(2)	(3)	(4)	(5)	(6)
1) Egg yolk volume	1.00	0.55	0.53	0.36	0.43	0.59
2) Length at hatching		1.00	0.58	0.45	0.32	0.42
3) Yolk volume at hatching			1.00	0.80**	0.08	0.54
4) Oil volume at hatching				1.00	0.13	0.68*
5) Age at hatching					1.00	0.57
6) Posthatching lifespan						1.00

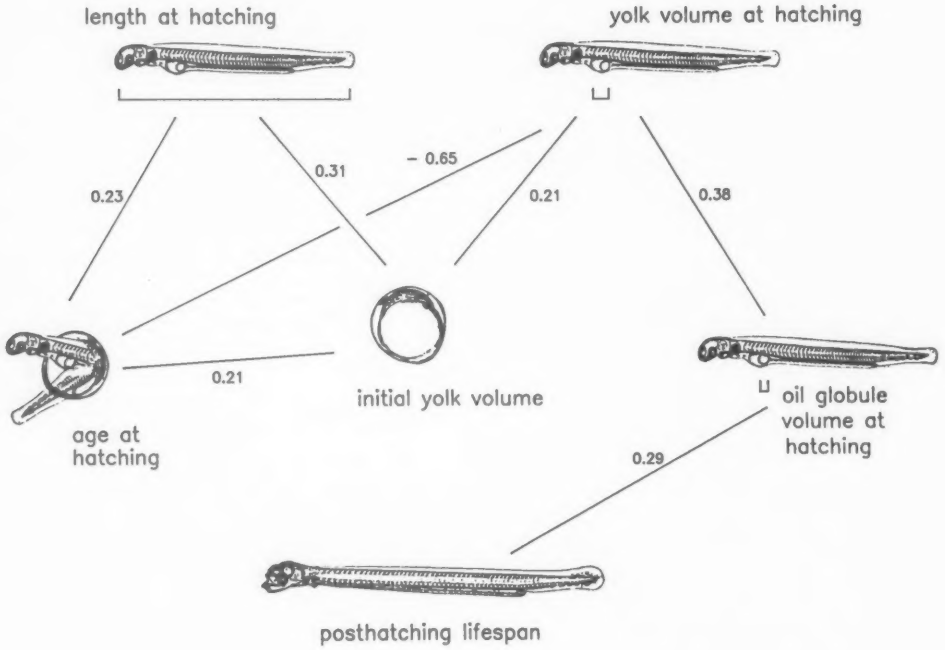

FIGURE 1.—Early life history traits of capelin, *Mallotus villosus*, subjected to analyses and the within-individual partial correlations between traits. Only significant correlations are shown ($P < 0.05$, df = 126).

ative correlations between traits. Second, while the correlation between yolk volume and oil globule volume at hatching and between oil globule volume and posthatching lifespan remained significant ($P < 0.05$), the magnitude of the correlations between posthatching lifespan and all other ELH traits approached significance. This pattern of correlations derived from family averages suggests that offspring from eggs with large yolk volumes are larger at hatching, hatch later, have larger yolk reserves and oil globules at hatching, and live longer than do offspring of females producing eggs with less yolk. This pattern is consistent with results of most previous reports based on average trait values.

Female Effects on ELH Traits

Initial egg yolk volume varied among females (Fig. 2). Female identity significantly influenced the set of six ELH traits (Wilk's $\lambda = 0.0001$, $F = 6.1$, df = 54, 70, $P < 0.0001$). Initial yolk volume and oil globule volume at hatching were the predominant traits contributing to among-female differences (Table 2). Univariate ANOVAs supported the MANOVA result; all traits varied significantly among females and the percentage of variance due to female was greatest for initial yolk and oil globule volume at hatching (Table 2). None of the family-averaged ELH traits was significantly correlated with female size. However, the average initial yolk volume of the egg was directly related to condition and lipid indices of the female (Table 2).

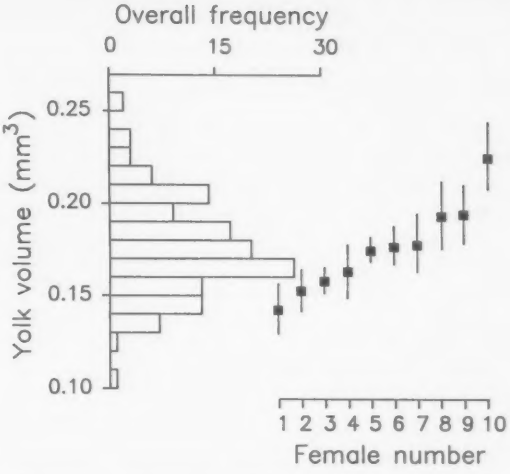

FIGURE 2.—Overall frequency distribution of initial egg yolk volumes and partitioned variation (means ± 2 SD) of yolk volumes by female for capelin, *Mallotus villosus*. A total of 142 eggs were measured from 10 females. Females are ranked by average yolk volumes of their eggs.

DISCUSSION

Correlations Between ELH Traits

Our observations of positive within-individual relationships between initial yolk volume and

TABLE 2.—Contributions of early life history traits (ELH) of capelin, *Mallotus villosus*, to the rejection of the null hypothesis of no female effect, and correlations between these traits and properties of female parents used. (1) Correlations between ELH trait means and the standardized discriminant function that maximized among female differences. (2) Percentage of total variance in each ELH trait due to female effect. Correlation between ELH trait means and female size (3), female condition index (4), and female lipid index (5). The magnitude of the correlation between ELH traits and the discriminant function reflects the contribution of a trait to rejection of the multivariate null hypothesis of no female effect. The eigenvalue associated with this discriminant function accounted for >77% of the variation among the ELH traits. * $P < 0.05$, ** $P < 0.01$.

	Egg yole volume	Length at hatching	Yolk volume hatching	Oil volume hatching	Age at hatching	Posthatch lifespan
1) Discriminant function	0.43	0.15	0.11	0.35	0.10	0.21
2) % variance	71.30	17.21	2.91	66.67	12.01	24.39
3) Female size						
SL	0.36	0.00	0.35	0.30	−0.41	−0.05
Wet somatic weight	0.61	0.18	0.53	0.43	−0.22	0.24
4) Female condition	0.65*	0.22	0.57	0.46	−0.17	0.29
5) Female lipid	0.85**	0.44	0.43	0.31	0.34	0.55

hatchling length, and between initial yolk volume and yolk volume at hatching agree with most previous reports based on grouped data (reviewed in Blaxter 1988). The positive relationship between initial yolk volume and age at hatching differs from the generally reported pattern of no association. Moreover, the increase in length with age at hatching we observed is contrary to that reported by Bengtson et al. (1987) who analyzed daily hatching cohorts within families. Hatching late, however, appears to occur at the expense of yolk reserves (Fig. 1). This negative relationship was not present in the correlations based on family averages (Table 1).

Neither initial yolk volume, length at hatching, nor yolk volume at hatching was related to posthatching lifespan when evaluated within individuals. This contrasts both with our correlations based on family averages and with previous generalizations (from group averages) that large initial egg size leads to hatchlings that survive longer in the absence of food (Blaxter 1988). The only association with posthatching lifespan that we detected was the direct influence of oil globule volume at hatching. Our data indicate that if all else were held constant, an increase in oil globule volume delays the time to starvation of individual larvae. This prolonged posthatching lifespan should increase the chances of encountering suitable food before irreversible starvation and, thus, the chances of survival. Lipids, whether aggregated in oil globules or dispersed throughout the yolk, appear to serve primarily as energy reserves (Blaxter 1969). Conservation of oil globules (relative to yolk) has been reported for species that have oil globules in their yolk sacs (e.g., May 1971; Bagarinao 1986) although oil globules may also serve to regulate buoyancy.

A variety of evidence argues for advantages of large size at hatching (a positive correlate of initial yolk volume). Larger larvae have greater mouth widths (Shirota 1970), have greater success in establishing feeding (Knutsen and Tilseth 1985), are more effective predators (Blaxter and Staines 1970; Hunter 1981), consume a greater range of prey sizes (Hunter 1981), and have higher survival when predators are absent (Rosenberg and Haugen 1982; Henrich 1988) or present (Lilleland Lasker 1971; Bailey 1984; Folkvord and Hunter 1986; Purcell et al. 1987). Although many of these studies compared larvae of two or more groups that differed in age as well as size, the results are likely to apply to the finer size differences among contemporaries. Mortality has also been reported to be size specific and to be concentrated early in the life cycle in natural populations (Crecco et al. 1983; Smith 1985; Rice et al. 1987; Savoy and Crecco 1988).

The cost of producing large eggs is frequently evaluated under the assumption of a trade-off between egg size and egg number (Svardson 1949; Smith and Fretwell 1974). This assumption has led to optimality derivations for balances between size and number of eggs under given conditions. Observed patterns of size and number of eggs among species, populations, or reproductive modes are then evaluated in light of the predicted optima (Ware 1975; Sargent et al. 1987; Tanasichuk and Ware (1987)). The correlations between ELH traits we observed suggest that egg size expresses reciprocity with other ELH traits to which optimality methods may be applied. For example, a corollary of the direct relationship between length and age at hatching in capelin is that an inverse relationship exists between length at and developmental rate to hatching (the reciprocal of age at hatching). If daily mortality rates are greater in the embryonic than in the larval period, an extended embryonic period is seen as a cost of being large at hatching.

This optimality approach is inherently deterministic. It does not explicitly admit within-population and within-female variation in egg size (Fig. 2) and in other ELH traits we observed. Rather, this variation is viewed as failure to achieve the optimal trait value or combination of trait values. In contrast, we consider trait variation itself to be adaptive. For capelin, the emergence of larvae from their intertidal incubation sites into the nearshore water is linked to the episodic occurrence of relatively warm water and nearshore turbulence, generated by onshore winds and coastal water mass exchanges (Frank and Leggett 1981a, 1983; Taggart and Leggett 1987b). The attainment of a developmental stage from which an embryo can be induced to hatch (e.g., through a sudden rise in temperature and/or turbulence) or its nutritional state at the time of emergence, if previously hatched (Frank and Leggett 1982), are important determinants of survival during early pelagic life. However, the intertidal incubation zone is variable for capelin in three fundamental ways. First, temperature directly influences developmental rates of embryos. Local temperatures in the intertidal substrate oscillate up to 10°C (Frank and Leggett 1981b) with tidal cycle. Thus, there are large microsite differences in

temperatures and developmental rates. Second, the small particle substrate to which eggs adhere is motile, mixing in all three dimensions with wave action. Third, onshore winds promote hatching and/or release of larvae from these beaches, yet their frequency is highly variable within and between years (Frank and Leggett 1981a, 1983; Leggett et al. 1984; Taggart and Leggett 1987b). From the maternal perspective, the time of the transition of her offspring from beach residence to the pelagic mode is unpredictable owing to these three sources of variation. It appears unlikely that a single optimal solution exists for developmental rate, size at hatching, or energy reserves. Additional examples of intrapopulation and intraclutch variation in early life history traits, and of theoretical bases for the maintenance of this variation in unpredictable environments, is provided in Capinera (1979) and Kaplan and Cooper (1984).

Female Effects on ELH Traits

Variation in egg quality is a sum of genetic and environmental factors. We have no evidence that egg size is heritable in capelin. We did not detect a male effect or heritable variation in size at hatching in another study involving 11 male capelin each mated with 3 females (Chambers and Leggett unpubl. data), yet there, as here, significant differences among females were evident in both initial egg and hatchling sizes. Our determination of a direct relationship between condition and lipid indices of females, and initial egg yolk volume probably reflects a predominant environmental component to the observed variation in egg quality (yolk volume) and its correlates. The degree of influence from environmental sources of maternal effects on ELH traits probably depends largely on conditions experienced by a female during the time that energy is being acquired and converted towards oogenesis, particularly her feeding rate (Hislop et al. 1978) and encountered temperatures (Tanasichuk and Ware 1987). If so, these largely nongenetic maternal effects have the potential to modulate the expression of critical ELH traits and modify the survival pattern that would otherwise be exhibited if the initial provisioning of yolk reserves were at par throughout the population. Well-endowed individuals could thus be buffered against selection in the yolk-dependent period with, perhaps, residual effects later in larval life. The inverse correlation between size of mother and age at smoltification of her progeny in sockeye salmon, *Oncorhynchus nerka*, as reported by Bradford and Peterman (1987) may be such a residual effect.

Covariation Within Individuals and Variation Within Groups

Relationships we observed between ELH traits clearly show that simple correlations based on group data may support, but may also be inconsistent with inferences drawn from analyses at the individual level. Only estimates of variation and correlations between traits that are based on individual-level observations are grounded on the same scale that natural selection primarily acts (Sober 1984). Caution must be exercised when extrapolating from group differences or correlations based on averages to influences of one trait on another, to potential advantages conferred on individuals, to dynamics of populations, or to evolution of life histories.

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A Laboratory Study of the Bioenergetics of Larval Walleye Pollock, *Theragra chalcogramma*

Yoh Yamashita and Kevin M. Bailey

ABSTRACT: Rates of growth, oxygen consumption, and ingestion were measured for larval walleye pollock, *Theragra chalcogramma*, in the laboratory. These measurements were used to relate assimilation and growth efficiencies to larval age (and size) and prey ration level. Larval growth was 0.06 mm/d during the transition from endogenous to exogenous food (days 4–16), and increased to 0.16 mm/d (days 19–21). Ingestion ranged from 24 to 58% body dry weight/d. Oxygen consumption rates were measured and used to partition total daily metabolic expenditures into four components: resting metabolism; SDA; lights-on generated nonfeeding activity; and active (feeding) metabolism, which accounted for 45.7, 13.3, 11.1, and 29.9% of the total daily metabolic rate, respectively. Net assimilation efficiency ranged from 24 to 64% and gross growth efficiency ranged from 9 to 35%, depending on larval age and size. Little difference was observed in efficiencies at low and high ration levels. The daily caloric requirement to support metabolism and growth of first-feeding larvae was calculated at 0.16 calories, which is equivalent to 76 copepod nauplii. This value is higher than ingestion estimates from field studies.

Capture and transformation of energy into body mass is especially critical during the larval stage of marine fishes. Specific growth rate is highest during this stage and weight may increase by three orders of magnitude (Smith 1985; Houde 1987). Furthermore, duration of the larval stage, as regulated by growth rate, is recognized as a crucial factor in determining year class strength (Houde 1987; Miller et al. 1988). Growth efficiency, the proportion of ingested energy used in growth, depends on a number of factors including environmental conditions, prey quality, prey abundance, and larval size and age.

Walleye pollock, *Theragra chalcogramma*, is the most abundant commercial species in the northeastern Pacific Ocean, comprising 80% of the total groundfish catch (Bakkala et al. 1986). Several studies have evaluated the bioenergetics of late larvae, juveniles, and adults (Fukuchi 1976; Nishiyama 1981; Harris 1985; Smith and Paul 1986; Dwyer et al. 1987; Smith et al. 1988) but there are relatively few studies of bioenergetics of early larvae, and their growth efficiency is unknown. Incze et al. (1984) reviewed the early life history of this species and calculated daily ration based on literature-derived values of growth and respiration. Clarke (1984) made a similar estimate. Early studies of larval walleye pollock respiration were limited because larvae were not successfully grown in the laboratory. Likewise, estimation of larval growth, determined from otolith ageing, was limited by the lack of daily increment validation. Recently, walleye pollock larvae have been successfully reared in the laboratory (Bailey and Stehr 1986), and daily growth increments on otoliths have been validated (Nishimura and Yamada 1984; Bailey and Stehr 1988).

In the present study we estimate components of the energy budget of larval walleye pollock reared in the laboratory. These components include rates of ingestion, growth, and metabolism. Oxygen consumption was measured at different levels of activity in order to model daily metabolic costs. We also calculated efficiencies of assimilation and growth for larvae as influenced by ration and age.

MATERIALS AND METHODS

Rearing of Larvae

Experiments were carried out from March to May 1988. Eggs from ripe females, collected in Puget Sound, were fertilized and reared according to methods described by Bailey and Stehr (1986). Yolk-sac larvae were transferred to 120 L black fiberglass tanks set in a water bath. Initial stocking density was 1,200 larvae per tank. Overhead fluorescent lights, on a 14 h

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light:10 h dark cycle, illuminated the tanks at an intensity of 5–8 $\mu E/s/m^2$ just below the water surface. Water was replaced with filtered seawater at 10–15% per day. Larvae were fed rotifers, *Brachionus plicatilis*, that had been cultured on a mixture of *Isochrysis* spp., *Chaetoceros* spp., and yeast.

Three rearing experiments were done using larvae hatched from eggs collected on different days. In the first experiment, growth, rate of gastric evacuation, and daily ration were measured in larvae reared at high (11.2 ± 1.4 SD rotifers/mL) and low (2.0 ± 1.4 SD rotifers/mL) rations. Mean temperature in both tanks was 6.4°C (±0.2 SD). In the second and third experiments, oxygen consumption rates for larvae were determined. Rotifer densities were maintained at about 10 individuals/mL. Average temperature was 6.3° ± 0.1°C (SD). Temperatures of 6.0°–6.5°C are common in Shelikof Strait (Gulf of Alaska) in May when early-stage larval walleye pollock are most abundant (Kendall et al. 1987).

Growth Rates

The standard lengths (SL) of live larvae were measured to the nearest 0.03 mm using a dissecting microscope, the gut contents were removed, and the larvae were dipped in distilled water and then dried for 24 hours at 60°C. Dry weights were measured to the nearest 0.1 μg on a Cahn 25 electrobalance. Yolk-sac dry weight was estimated as the difference between the mean dry weight of larvae with yolk sacs and the mean dry weight of larvae whose yolk sacs had been excised. Instantaneous rate of growth (G) and relative rate of growth (K) were estimated from the following equations (Ricker 1975):

$$W_t = W_0\, e^{G \cdot t}, \text{ where}$$

$$G = (\ln W_t - \ln W_0)/t, \text{ and}$$

$$W_t = W_0(1 + K)^t, \text{ where}$$

$$K = e^G - 1.$$

W_0 is the initial dry weight (in μg) and W_t is the dry weight at time t (in days). Daily specific growth rate is defined as G (× 100%) (Laurence 1975).

In order to compare subarctic walleye pollock with the subtropical larvae used in other studies, we used methods and analyses to parallel those of Houde and Schekter (1981, 1983) and Theilacker (1987). One major difference was that we did not use nonfeeding larvae, but sampled randomly from feeding larvae. Theilacker (1987) used all randomly sampled larvae including nonfeeding larvae to estimate ingestion and growth; Houde and Schekter (1981, 1983) sampled only feeding larvae to measure ingestion, and feeding and nonfeeding larvae to measure growth. In some species, relatively few larvae may feed on cultured prey at low densities in laboratory conditions. This may not have been a problem in the Theilacker (1987) and Houde and Schekter (1981, 1983) studies. In our studies we considered feeding incidence as a behavioral problem not to be included as a factor in a study of energetic efficiency. Since our objective was to compare efficiencies of larvae feeding at high and low rations, we opted to exclude nonfeeding larvae from our samples.

Evacuation Rates

Instantaneous rates of gastric evacuation were measured for actively feeding larvae. Larvae were fed rotifers, dyed with Alcian Blue, at prey densities of 2.2–4.0/mL. After 1.2–1.5 hours larvae were transferred to a tank containing undyed rotifers either at 11.1–15.6 rotifers/mL for the high ration treatment or at 0.8–1.8 rotifers/mL for the low ration treatment. Larvae were sampled at intervals from 20 to 60 minutes, and widths of rotifers and their degree of digestion determined. Mean gut-clearance times were estimated for the duration between ingestion and defecation of dyed rotifers.

Theilacker and Kimball's (1984) method was used to determine that 54% of rotifer dry weight was lost after 4 hours of digestion. Based on that loss, three correction factors for the degree of rotifer digestion were used to calculate ingestion: 0.9 for recently ingested rotifers; 0.7 for moderately digested rotifers, which still had abundant chlorophyll from ingested phytoplankton; and 0.5 for well-digested rotifers with almost no chlorophyll. The total dry weight of dyed rotifers in the gut was determined by summing the product of the width-specific dry weight for each rotifer (Theilacker and Kimball 1984) and the appropriate digestion factor. Data were fitted to the model:

$$A_t = A_0\, e^{-R \cdot t}$$

where A_0 and A_t are the ratios of the dry weight

of dyed rotifers in the gut to larval dry weight at times 0 and t (in hours). R is the calculated instantaneous rate of gastric evacuation.

Ingestion Rate

About 10 larvae from both high and low prey-ration tanks were sampled 5 times each day at 1.5–3 h intervals during the light period. Prey were removed from larval guts, counted, their widths measured, and the degree of larval digestion determined. Total gut content in dry weight per larva was determined by summing the product of the width-specific dry weights of rotifers and digestion factors.

Asymptotic curves of the form

$$S = S_{\max} \times (1 - e^{-F \cdot t}),$$

were used to describe ingestion rates, where S is the ratio of gut content to larval dry weight (× 100%) at time t (in hours) after initiation of light period, $S_{\max}$ is the asymptotic gut content (%) and F is the instantaneous rate of gut filling.

Weight-specific daily ration (I) as a percent of body weight was estimated for larvae using the Elliot and Persson (1978) model:

$$I = \sum_{i=1}^{m} (S_i - S_{i-1}\, e^{-R \cdot t_i})\, R t_i / (1 - e^{-R \cdot t_i})$$

In this model, t_i is the duration of each time interval (i) in hours; S_i is the mean gut content at the end of interval (i) as a percent of larval dry body weight; and m is the total number of intervals during a light cycle. S_0 was assumed to be 0; and S_m, the gut contents at the end of the light period, was approximated as $(S_{m-1} + S_{m-2})/2$.

Metabolic Rates

Oxygen consumption rates were measured using the micro-Winkler technique (Carrit and Carpenter 1966; Strickland and Parsons 1972). We assumed that there are four metabolic activity levels: 1) resting or basal (M_{re}); 2) routine (M_{ro}), which includes M_{re} plus a cost for an lights-on generated activity; 3) feeding (M_{fn}), which includes M_{re} and an additional cost for specific dynamic action (SDA); and 4) active (M_a), which includes M_{re} plus increments due to lights-on activity and SDA, and an additional cost of pursuing and capturing prey.

Oxygen consumption rates for the different levels were measured as follows:

1. M_{re}: larvae were allowed to void their guts for 24 hours and were then incubated in dissolved oxygen (DO) bottles for 24 hours in complete darkness.
2. M_{ro}: larvae were allowed to void their guts for 24 hours and were incubated for 12 hours in the light during daytime.
3. M_{fn}: larvae with full guts after a 12 h feeding period were incubated for 12 hours in the dark during nighttime.
4. M_a: larvae with a few rotifers in their guts were incubated for 12 hours in the light during daytime with rotifers at a density of 5 individuals/mL.

Sixty milliliter DO bottles were used for conditions 1–3 and 300 mL DO bottles for condition 4. The bottles were set in a black container filled with seawater. Each bottle contained 5–30 larvae depending on larval and bottle size. Three to five replicates with control blanks (containing rotifers in condition 4) were carried out for each age and condition at 6.2 ± 0.1(SD)°C. Light intensity at the top of bottles was 6–9 $\mu E/s/m^2$ during the light period.

The value for M_{re} used here may be larger than that of other studies that use anesthetized larvae (Holliday et al. 1964; de Silva and Tytler 1973; Davenport and Lönning 1980; de Silva et al. 1986), as larvae normally move at night, even though at a much reduced level (Batty 1987). However, our method eliminates possible biases involved with the use of anesthetics. The active metabolism (M_a) was probably underestimated owing to restricted activity and feeding in 300 mL bottles, and to effects of handling. Restricted feeding in DO bottles was evidenced by the lower number of ingested rotifers in guts at the end of experiments compared with the number of ingested rotifers in the guts of larvae in the 120 L tank.

Energy Budget

Energy budgets (in calories per day) were determined for feeding larvae from 7 to 21 days from posthatching using the equation:

$$I = G + M + E$$

where I = ingestion, G = growth, M = metabolism, E = nitrogenous and fecal excretions. Excretion was not measured, but the total loss of

wastes can be estimated by difference. Also, the efficiencies we used—G/I, M/I, $(G + M)/I$, and $G/(G + M)$—are not dependent on excretion measurements.

Average daily ingestion in dry weight was calculated as (mean larval weight) × (weight-specific daily ingestion). Dry weight of rotifers was converted to caloric equivalents using a factor of 4.4 cal/mg (Theilacker and Kimball 1984).

Daily growth of larvae at (t_i) was calculated from the daily growth rate (K) for the interval $t_i - t_{i+1}$. Dry weight was converted to calories using a factor of 5.077 cal/mg estimated for larval walleye pollock (Fukuchi 1976; Harris et al. 1986). Fukuchi (1976) also provided constants for converting dry weight to net weight, nitrogen, and carbon (8.59, 0.092, and 0.131, respectively).

Daily O_2 consumption rate (M_{24}) μL/d/individual (14 h light and 10 h dark photoperiod) was calculated as

$$M_{24} = 2 \times (M_{ro}) \times 14 + (M_{fn}) \times 10.$$

Oxygen consumption was converted to calories using an oxycaloric equivalent of 4.63 cal/mL O_2 (Brett and Groves 1979). We attempted to measure active metabolic rates as described above, but larvae did not actively feed. Therefore, active metabolic rate was approximated as twice the routine metabolic rate (Houde and Schekter 1983; see also Lasker 1970).

RESULTS

Growth rates

Hatching began 7–8 days after fertilization, and by 3–5 days later more than 80% of the eggs had hatched. The day of 50% hatching was designated as the day of hatching for all larvae.

By day 6 after hatching, yolk-sac dry weight was less than 5% of the initial weight; the yolk was absorbed completely by days 11–15. A small percentage of larvae started feeding on day 5 and most larvae started on day 6. Therefore, day 6 was designated as the onset of feeding. Newly hatched yolk-sac larvae averaged 3.80 mm (SL) and 55.5 μg (dry weight), and by day 4 (existing only on yolk) averaged 4.59 mm and 47.5 μg. By day 21, high ration larvae grew to 6.02 mm (mean SL) and 120.9 μg (mean dry weight) and low ration larvae grew to 5.94 mm and 116.2 μg. The linear growth rate in SL during yolk-sac period (from days 0 to 4) was 0.20 mm/d; it decreased to 0.07 (high ration) and 0.06 (low ration) mm/d during the transition from endogenous to exogenous energy (from days 4 to 16), and then increased to 0.13 (high ration) and 0.12 (low ration) mm/d (from days 16 to 21). Specific growth rate in weight from days 7 to 21 was estimated as 6.71%/d for high ration and 6.04%/d for low ration larvae. Standard length (SL) and dry weight (W) were related by a power function:

$$\text{high ration: } W = 0.1261 \times \text{SL}^{3.812} \quad (r = 0.980 \quad N = 45)$$

$$\text{low ration: } W = 0.1754 \times \text{SL}^{3.615} \quad (r = 0.979 \quad N = 45).$$

Although the length-specific weight gain of high ration larvae tended to be greater than that of low ration larvae, the difference between the two food levels was not statistically significant (F-test for difference between two linear regression slopes, $P > 0.1$).

Evacuation Rates

The weight of dyed rotifers in larval guts decreased exponentially for the first 5–7 hours, then the rate of larval digestion slowed. Instantaneous rates of gastric evacuation (R) were estimated from the exponential phase for 8–9 d old larvae and 17–21 d old larvae. Rates for younger larvae were higher than those for older larvae, and high ration larvae had higher evacuation rates than low ration larvae (Table 1). The same tendencies were found in gut clearance times. Coiling of the midgut is initiated at about 5.2 mm SL (day 14) and is completed at about 5.8 mm (day 20), effecting the differentiation of foregut and intestine. The relationship between R and the percentage of larvae having coiled midgut (>5.5 mm SL) showed higher evacuation rates for larvae without the coiled gut.

Ingestion Rate

By our observation, larval walleye pollock are continuous feeders. There was no significant difference (Chi-square test: $P > 0.1$) between widths of rotifers in larval guts and widths of rotifers in cultures provided to larvae as food.

The ratio of gut contents to larval dry weight generally increased asymptotically with time (Fig. 1). Maximum mean percent of gut contents measured after 14 h feeding were 6.9% and 5.1% for 7 d old high ration and low ration larvae, respectively. These values increased to about 10% by day 13 and thereafter remained fairly

TABLE 1.—Instantaneous rates of gastric evacuation and gut clearance time related to age and feeding condition of larval walleye pollock at 6.4°C. Data were fitted to the equation: $A_t = A_0\, e^{-Rt}$ (see text). Also shown is the percent of larvae in the experiments greater than 5.5 mm SL, as an indicator of those with midgut coiling.

Age (d)	Feeding condition	Instantaneous evacuation rate (R)	A_0	Gut clearance time (h)	% Larvae >5.5 mm SL	N
8	high ration	0.473	3.399	5.3	0	93
9	low ration	0.415	2.571	6.1	0	97
17	low ration	0.263	2.601	10.1	64	61
18	high ration	0.256	3.082	9.6	79	61
21	high ration	0.327	4.743	9.4	73	40

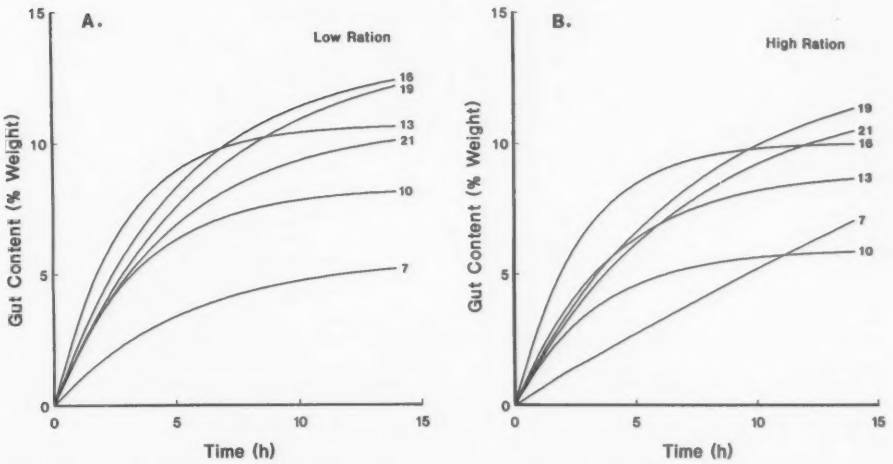

FIGURE 1.—Curves to describe food intake of low ration (A.) and high ration (B.) pollock larvae. Data were fitted to the equation: $S = S_{max} \times (1 - e^{-F \cdot t})$, where S is percent dry weight of gut contents to larval dry weight at time t (h) after initiation of light period; S_{max} is the asymptotic gut content (%); and F is the instantaneous rate of gut filling. Numbers after each line indicate age in days.

constant (Table 2). About 10–12% seems to be the maximum capacity of larval pollock guts within the range of stages examined. These measured maximum values are close to S_{max} values predicted from the asymptotic gut content curve (Table 2). The value for 7 d old high ration larvae was an exception; the ingestion curve appeared to be nearly linear and the resulting S_{max} high (Fig. 1; Table 2)

To estimate daily ration, instantaneous rates of gastric evacuation under specific age and feeding conditions were taken from Table 1. At day 7, one day after feeding commenced, weight-specific daily ration was low, about 24–29% (Table 2). Daily ration increased to a level of about 55% at days 13–16. In spite of the observed constant values of maximum percent gut contents with age, daily ration decreased to about 35% by day 21. The difference in daily ration between the high and low ration conditions was not significant (ANOVA, $P > 0.1$).

Metabolic Rates

Results of oxygen consumption rate measurements are summarized in Table 3. From day 0 to day 4 after hatching there was no remarkable difference in respiration between daytime (M_{ro}) and night (M_{re}). After day 6, when most larvae commenced feeding, O_2 consumption rate increased as age and weight of larvae increased, and M_{ro} was from 25 to 68% higher than M_{re}. O_2 consumption rates in the four conditions were significantly different (ANOVA, $P < 0.01$).

TABLE 2.—Summary of ingestion experiments for larval walleye pollock. S_{max} is estimated asymptotic gut content and F is instantaneous rate of gut filling. Parameters were estimated from the equation: $S = S_{max} \times (1 - e^{-Ft})$ (see text).

Diet	Age (d)	N	Asymptotic curve model: Instantaneous rate of gut filling (F)	Asymptotic[1] gut content (S_{max})	Estimated[1] gut content after 14 h feeding	Max mean gut content of reared larvae (%)	Daily ration (%)
High ration	7	30	0.017	33.5	7.1	6.9	29.4
	10	37	0.292	6.0	5.9	6.4	37.3
	13	41	0.250	9.0	8.7	9.8	50.9
	16	35	0.371	10.1	10.0	10.8	53.2
	19	40	0.138	13.3	11.4	11.2	42.1
	21	41	0.141	12.2	10.5	10.9	37.0
Low ration	7	32	0.185	5.6	5.2	5.1	24.2
	10	37	0.288	8.3	8.1	8.5	42.3
	13	41	0.362	10.7	10.6	11.0	58.5
	16	35	0.196	13.3	12.4	11.5	49.6
	19	40	0.162	13.6	12.2	11.3	38.1
	21	41	0.205	10.7	10.1	9.8	33.7

[1]Percent of gut content to larval dry weight.

TABLE 3.—Oxygen consumption rates at 6.2°C for larval walleye pollock at different experimental activity levels. The number of replicates per treatment was 3-5. Values in parentheses are for yolk-free weights.

Age (d)	Mean dry weight (µg)	Oxygen consumption activity level: Resting (M_{re}) µL/h/ind	SD	µL/h/mg	Routine (M_{ro}) µL/h/ind	SD	µL/h/mg
0	54.2	0.068	0.011	1.25(2.06)	0.068	0.003	1.26(2.08)
3	53.1	0.082	0.008	1.55(1.89)	0.086	0.019	1.61(1.96)
4	48.3	0.076	0.004	1.58(1.72)	0.077	0.012	1.59(1.76)
6	47.6	0.083	0.008	1.74(1.76)	0.112	0.019	2.35(2.38)
11	55.1	0.098	0.009	1.78	0.123	0.037	2.24
14	68.1	0.104	0.026	1.53	0.140	0.023	2.06
19	87.9	0.129	0.021	1.47	0.217	0.064	2.47
20	89.8	0.137	0.030	1.53	0.226	0.022	2.52
23	131.3	0.212	0.026	1.61	0.269	0.051	2.05

Age (d)	Mean dry weight (µg)	Oxygen consumption activity level: Feeding (M_{fn}) µL/h/ind	SD	µL/h/mg	Active (M_a) µL/h/ind	SD	µL/h/mg
6	47.6	0.100	0.014	2.09(2.12)	0.136	0.016	2.87(2.91)
11	55.1	0.134	0.024	2.43	0.153	0.042	2.78
14	68.1	0.134	0.017	1.97	0.193	0.036	2.83
19	87.9	0.153	0.026	1.74	0.251	0.036	2.86
20	89.8	0.185	0.020	2.06	0.304	0.008	3.39
23	131.3	0.287	0.067	2.19	0.406	0.074	3.07

The relationships of O_2 consumption rate (µL/h/individual) and mean larval dry weight (W, in µg) of feeding larvae for the different metabolic levels were

$$M_{re} = 0.00276\, W^{0.8707} \quad (r = 0.844,\ n = 26)$$
$$M_{ro} = 0.00253\, W^{0.9699} \quad (r = 0.807,\ n = 27)$$
$$M_{fn} = 0.00308\, W^{0.9059} \quad (r = 0.845,\ n = 25)$$
$$M_{a} = 0.00176\, W^{1.1154} \quad (r = 0.906,\ n = 25)$$

The metabolic mass exponents, particularly for routine metabolism, were close to unity.

For prefeeding larvae, weight-specific O_2 consumption rate (μL/h/mg) increased with age (Table 3). This is probably associated with increasing somatic tissue, because yolk is thought to be nonrespiring (Rombough 1988). Weight-specific rates, using yolk-free dry weight, decreased with age. As the eye became functional, at days 5 and 6, a rapid rise in routine metabolism followed the increase in light-stimulated activity. From days 6 to 23 there were no significant trends in the dry weight specific O_2 consumption rate with age for any treatments (ANOVA with regression, $P > 0.1$).

By difference ($M_{ro} - M_{re}$), lights-on generated activity of feeding larvae accounted for an average O_2 consumption of 0.67 μL/h/mg. Nighttime SDA ($M_{fn} - M_{re}$) accounted for 0.47 μL/h/mg, and feeding activity associated with hunting and capture of prey ($M_a - M_{ro} - 0.47 - 0.67$) accounted for 0.22 μL/h/mg. Given that the active-feeding metabolic rate was probably underestimated by our technique as noted previously, and that the active metabolic rate can be estimated as $2 \times M_{ro} = 4.56$ μL/h/mg, the above increment for active metabolism would be 1.81 μL/h/mg.

Energy Budget

Energy budget components and efficiencies are given in Table 4. Gross growth efficiency ($G/I \times 100$) ranged from 13.2 to 34.5% for high ration and from 9.1 to 32.6% for low ration larvae. The relationship of G/I and age was a U-shaped function with low efficiency in middle stages (Fig. 2). The ratio of metabolizable energy to ingestion ($(G + M)/I \times 100$) is termed net assimilation efficiency. Net assimilation efficiency also showed a U-shaped relationship with age, ranging from 30.5 to 58.4% and from 24.4 to 63.5% for high ration and low ration larvae, respectively. The ratio of the growth component to metabolizable energy ($G/(G + M) \times 100$) gradually increased from 40-42% at day 7 to 55-59% at day 21.

DISCUSSION

The growth rates of walleye pollock larvae in our experiments compared favorably to those of

TABLE 4.—Daily energy budget components and efficiencies of larval walleye pollock. H and L indicate high ration and low ration levels, respectively.

Age:	7	7	10	10	13	13	16	16	19	19	21	21
Feeding condition	H	L	H	L	H	L	H	L	H	L	H	L
Mean SL (mm)	4.77	4.81	4.94	4.96	5.13	5.15	5.38	5.35	5.71	5.69	6.02	5.94
Mean dry weight												
(W_D)(μg)	46.5	48.6	54.0	57.3	67.6	68.4	80.2	78.1	98.0	96.6	120.9	116.2
(cal)[1]	0.236	0.247	0.274	0.291	0.343	0.347	0.407	0.397	0.498	0.492	0.614	0.590
Ingestion (I)												
(μg/d)	13.66	11.75	20.14	24.26	34.43	40.00	42.67	38.73	41.28	36.95	44.67	39.16
(cal/d)[2]	0.060	0.052	0.089	0.107	0.151	0.176	0.188	0.170	0.182	0.163	0.197	0.172
Growth (G)												
(μg/d)[3]	2.37	2.72	4.21	3.50	3.99	3.08	5.53	5.86	10.88	9.21	13.42	11.04
(cal/d)[2]	0.012	0.014	0.021	0.018	0.020	0.016	0.028	0.030	0.055	0.047	0.068	0.056
Metabolism (M)												
(μL O_2/d)	3.94	4.11	4.57	4.85	5.72	5.79	6.79	6.61	8.29	8.29	10.23	9.84
(cal/d)[4]	0.018	0.019	0.021	0.022	0.026	0.027	0.031	0.031	0.038	0.038	0.047	0.046
G/I[5] (%)	20.0	26.9	23.6	16.8	13.2	9.1	14.9	17.6	30.2	28.8	34.5	32.6
M/I[5] (%)	30.0	36.5	23.6	20.6	17.2	15.3	16.5	18.2	20.9	23.3	23.9	26.7
$(G + M)/I$[5] (%)	50.0	63.5	47.2	37.4	30.5	24.4	31.4	35.9	51.1	52.1	58.4	59.3
$G/(G + M)$[5] (%)	40.0	42.4	50.0	45.0	43.5	37.2	47.5	49.2	59.1	55.3	59.1	54.9
I/W_D[5] (%)	25.4	21.1	32.5	36.8	44.0	50.7	46.2	42.8	36.5	33.1	32.1	29.2

[1]Larval dry weight was converted to calories by a factor of 5.077 cal mg^{-1}.
[2]Rotifer dry weight was converted to calories by a factor of 4.4 cal mg^{-1}.
[3]Daily growth was calculated using the relative rate of growth (K) at each day interval.
[4]Oxygen volume was converted to calories by a factor of 4.63 cal mL^{-1} O_2.
[5]Efficiencies were expressed on caloric basis.

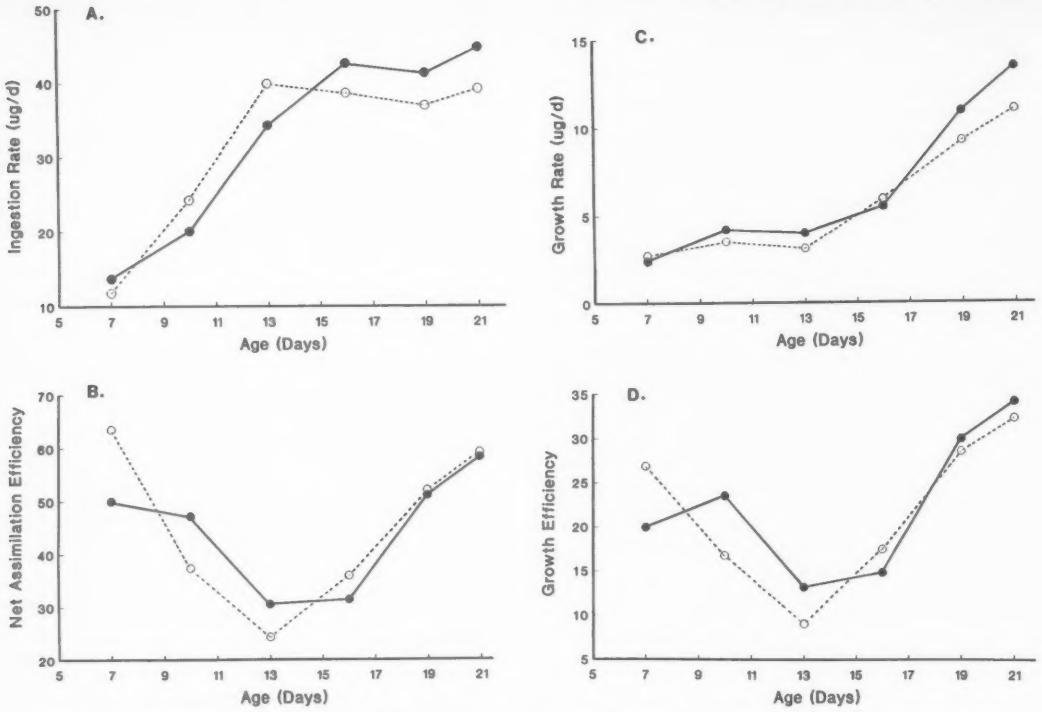

FIGURE 2.—Ingestion rates (A.); net assimilation efficiencies (B.); growth rates (C.); and growth efficiencies (D.) of reared walleye pollock larvae. Closed circles and open circles indicate well fed and poorly fed larvae, respectively.

larvae caught at sea. In the laboratory, yolk-sac larvae from days 0 to 4 (posthatch) were growing 0.20 mm/d at 6.4°C. Growth rates decreased to 0.06 mm/d just after onset of feeding (4.8 mm SL) and increased to 0.16 mm/d from days 19 to 21 (5.8 mm SL). Growth rates of field-collected walleye pollock larvae, determined from otolith increments, ranged from 0.12 to 0.25 mm/d, linearized over ages 7–45 days (6.0–14.6 mm SL) for larvae caught in the Gulf of Alaska in 1983 (at 5.5°–7.0°C (Kendall et al. 1987)). In 1987 the growth rate of Gulf of Alaska walleye pollock larvae at 5.8 mm SL was 0.18 mm/d as determined from the growth equation given in Yoklavich and Bailey (1989). Growth of field-caught larvae, like laboratory-reared larvae, was slow at ages corresponding to the transition from endogenous to exogenous feeding. Specific growth in dry weight was 7%/d. This is somewhat slower than the wet weight-specific growth rates estimated from field-caught larvae at 10%/d (Fukuchi 1976; Nishiyama 1981). These weight-specific growth rates are much lower than those of subtropical species (from 15 to 50%/d) (Houde and Schekter 1983; Theilacker 1987), but they are similar to those of other subarctic species (Laurence 1975; 1978)

Decreased evacuation rates with increased larval size (and age) were closely related to the development of the digestive system, especially midgut coiling, which begins at about 5.2 mm SL (13–16 days) and is completed at about 5.8 mm (19–21 days). Our gut clearance times (5.3–6.1 hours) for first-feeding larvae fed rotifers are similar to the 5 hours found by Paul (1983) for pollock larvae fed copepod nauplii at 5.5°C. Generally these gut clearance times are considerably slower than those of warm-water species, e.g., northern anchovy at 1.15–1.5 hours (Theilacker 1987). Walleye pollock larvae with high ingestion rates in high prey densities had faster rates of gut clearance compared with those held in low prey densities. Furthermore, larvae with full guts placed in prey-free water had very slow clearance rates, indicating that continuous feeding facilitates movement of ingested prey through the guts.

Specific daily ration increased from 21 to 25% at day 7 to a peak value of 46-51% at days 13–16 as a function of increasing ingestion rates. It

declined to 29–32% at day 21 as a result of the longer gut clearance times discussed previously. The inverted U-shaped function observed here was also noted by Houde and Schekter (1981) while studying three species of subtropical larvae. Daily rations for warm-water species are considerably higher than those found in this study, ranging from 202 to 379%, 165 to 297%, and 121 to 234% per day on a caloric basis for bay anchovy, *Anchoa mitchilli*, lined sole, *Achirus lineatus*, and sea bream, *Archosargus rhomboidalis*, respectively (Houde and Schekter 1983); values of 26–70% were found for northern anchovy converted to a caloric basis from data in Theilacker (1987); and values of 42–160% on a dry weight basis for summer flounder, *Paralichthys dentatus*, (Buckley and Dillmann 1982).

Our values of routine metabolism at 6.2°C in Table 4 correspond quite closely to values for walleye pollock and cod found by other investigators. For example, our values of 2.24 and 2.06 μL/h/mg for 11 and 14 d old larvae are similar to values of 1.86 and 2.14 for 11 and 14 d old pollock larvae at 4°C found by Clarke (1984). Adopting a Q_{10} value of 2.3 (Brett and Groves 1979), Clarke's values are equivalent to 2.23 and 2.57 μL/h/mg at 6.2°C. Routine metabolic rates for young cod larvae at 5°C have been measured at 1.6 (Davenport and Lönning 1980) and at 1.8–2.0 μL/h/mg (Solberg and Tilseth 1984).

We attempted to partition metabolism into its component parts for estimating daily metabolic cost. From the equation for total daily metabolism, the four components—SDA, lights-on generated nonfeeding activity, resting metabolism, and feeding activity—accounted for 13.3, 11.1, 45.7, and 29.9% of the total daily metabolic expenditure. Because of the experimental nature of these measurements, they should be considered a first approximation, subject to refinement. For example, degradation of rotifers that were defecated in the DO bottles could have consumed some of the available oxygen and should be controlled for in future studies. Our values for resting metabolism may include some cost for biosynthesis because a 24 h period of nonfeeding acclimation time is probably not enough to eliminate the effect of SDA (Brett and Groves 1979). The value for active feeding metabolism seems high compared with the relatively inactive behavior of walleye pollock larvae. The assumption that active metabolic rate is twice the routine metabolic rate may have resulted in an overestimate of this component.

Net assimilation efficiency [$(G + M)/I$], ranged from 24 to 64% in our study, as a U-shaped function related to age. These efficiencies are low compared with generalized rates of 65–75% for young fish given by Ware (1975) and 73% for young carnivorous fish given by Brett and Groves (1979). However, the assimilation rate during larval life seems to change greatly during development, and rates are usually quite low for young larvae. For example, net assimilation efficiency for northern anchovy changed with increasing larval size from 44.4 to 65.7% for well-fed larvae (Theilacker 1987). Net assimilation efficiency for bay anchovy, lined sole, and sea bream ranged from 17.2 to 33.7%, 26.6 to 46.1%, and 37.2 to 67.6%, respectively, for different developmental stages of these fishes (Houde and Schekter 1983).

High assimilation efficiency during the first few days of feeding may be due partly to residual yolk contributing to "ingestion". Yolk is converted into body tissue very efficiently (Lasker 1962). Assimilation efficiency decreased to a low point at day 13 of our experiments. We suggest that development of the digestive system lagged behind that of behavioral feeding prowess, and that low assimilation efficiencies were linked to the growth lag observed during the transition from endogenous to exogenous food. Assimilation efficiency and growth rate increased when ingestion reached a maximum and the alimentary canal developed midgut coiling, resulting in longer gut clearance time.

Gross growth efficiency (G/I) ranged from 11 to 34% as a U-shaped function of age (and size). Houde and Schekter (1983) reported similar U-shaped functions with size ranging from 10.9 to 20.8% for bay anchovy, from 12.8 to 23.3% for lined sole, and from 21.4 to 41.3% for sea bream. Most values for larvae are suggested to be in the 5–40% range (Houde and Schekter 1983) or 14–41% range (Theilacker and Dorsey 1980). The efficiencies of pollock larvae are consistent with these ranges. Our gross growth efficiencies are lower than those of 30–47% found by Theilacker (1987) for well-fed northern anchovy larvae.

Growth rates, ingestion rates, assimilation efficiencies, and growth efficiencies determined from this study differed surprizingly little between high and low rations. These results indicate that larvae robust enough to successfully initiate feeding at low prey densities were able to maintain high rations, and furthermore that growth responded very little to increased prey density. Lower levels of ration used here may be

necessary to assess the influence of marginal feeding conditions on growth or assimilation efficiency. Although we did not monitor feeding incidence and survival closely, both were higher in the high ration treatments. Consequently, including nonfeeding larvae in our study probably would have made differences appear in growth and ingestion rates between ration levels. Paul (1983) found fairly high incidences of pollock larvae feeding at low densities on copepod nauplii; however, the extreme smallness (250–1,000 mL) of containers used in that study probably invalidates the results.

According to Nishiyama and Hirano's (1985) formula for estimating mean gut content as a percent of wet body weight, guts of field-caught larvae 6 mm in total length (TL) should contain about 2% body weight. By contrast, larvae in our experiments contained 10–12% dry body weight. These results would indicate that either larvae in the field are not consuming prey at maximum rates, or there is a problem with collecting larvae from the field. Pollock larvae could be defecating when captured with nets; however, we observed that walleye pollock larvae did not defecate when probed with a dissecting needle, in contrast to anchovy larvae (Yamashita in press).

We can approximate mean caloric consumption of pollock larvae caught in the Bering Sea from the data of Dagg et al. (1984), who estimated that at an average temperature of 4.5°C, larvae 5.2 mm in length ingest 18.3 copepod nauplii/d. The mean length of copepod nauplii eaten by pollock larvae (5.2 mm TL) is 0.22 mm, as estimated from equations given by Nishiyama et al. (1986), and an equivalent wet weight is 1.38 μg (Nishiyama and Hirano 1985). Assuming 70% water content (Ikeda 1970) and the caloric content of adult *Pseudocalanus* (Laurence 1976), the mean caloric content of the average naupliar prey would be 0.0021 calories. Daily ingestion of larvae in the study of Dagg et al. (1984) would be 0.038 calories. Assuming 50% assimilation efficiency, 0.019 calories are available for metabolism and growth. This value, however, does not meet even the daily caloric requirement of 0.023 calories for metabolism alone, at 4.5°C (converted from 0.027 calories for metabolism of 13 d old larvae, 5.1–5.2 mm SL, at 6.2°C with an assumption of $Q_{10} = 2.3$ from Brett and Groves 1979). A daily caloric ingestion of about 0.16 calories is required for growth and metabolism for this size of larva from the results of our study. This value would be equivalent to 76 nauplii. Of course, prey size and metabolizable energy content may vary significantly.

The mean number of copepod nauplii at the depth of their maximum abundance in the Bering Sea during normal first-feeding of pollock larvae is 10–20/L (Clarke 1984; Dagg et al. 1984). These values are low compared with previously reported ranges of naupliar densities in the sea (e.g., Houde 1978; Hunter 1981). We believe that the low prey density, low percentage of gut contents to body weight of field-caught larvae, and the energetic requirements of larvae compared with estimated ingestion rates from field studies indicate that pollock larvae, like anchovy (Lasker 1975), are probably subject to food shortages in the sea. Since the growth response of walleye pollock larvae (at the low temperatures used in this study and in the sea) is low, one would not expect to see periodic episodes of low ration expressed markedly in mean larval growth rates (Yoklavich and Bailey 1989), but episodes of low ration would be better assessed on an individual basis, using chemical or histological methods.

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Size-Specific Vulnerability to Predation and Sensory System Development of White Seabass, *Atractoscion nobilis*, Larvae

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ABSTRACT: The size-specific vulnerability of white seabass, *Atractoscion nobilis*, larvae (2.5–15.0 mm SL) to two types of fish predators—adult northern anchovy, *Engraulis mordax*, and juvenile white seabass—was examined in laboratory predation trials. Concurrent analyses were made of the developmental ontogeny of larval visual and mechanoreceptive systems. The proportion of larvae responding to or escaping attacks by either predator increased with larval size. There were no significant differences in proportions of larvae responding to or escaping attacks of either predator until larvae were 6.0–7.5 mm SL (early postflexion stage). At this size, larvae were better able to evade the slower, more discontinuous attacks of juvenile white seabass compared with the faster attacks of adult anchovy. Major developmental events occur during this larval stage, including rapid improvement in visual acuity, visual accommodation to distant objects, growth and stratification of the optic tectum, and large increases in the numbers of free neuromasts on the head and trunk. It is likely that at larval sizes >7 mm SL, the slower attacks of juvenile white seabass allow more time for larvae to process and integrate visual and mechanoreceptive sensory input from several modalities. White seabass larvae (and sciaenids in general) become more demersal in distribution during the late larval stages in nearshore southern California waters. This ontogenetic shift deeper into the water column may be related to predator-avoidance capabilities of the larvae, since most demersal planktivores exhibit some type of hovering, ambush, or discontinuous mode of predation similar to that of juvenile white seabass and attack at much slower speeds than pelagic, shoaling fish predators. As they shift downward, older white seabass larvae may maximize their predator-detection capabilities when encountering demersal fish predators.

For most marine and estuarine fishes, predation-induced mortality during early life stages may be crucial in determining year-class strength. Predation has long been recognized as an important potential regulatory mechanism in prerecruit life stages (Houde 1978, 1987; Hunter 1981, 1984), but many of the specific factors that influence predation rates on early life stages are not well understood (Bailey and Houde 1989).

One of the crucial aspects of predator/prey dynamics involves the developmental or physiological basis for capture and escape responses. Fish larvae possess several sensory systems presumed to be important in predator detection; these include visual, mechanoreceptive, and auditory systems. During early ontogeny, these sensory systems undergo rapid development, and the improvement in these systems is thought to be crucial in controlling vulnerability to predation (Hunter 1984; Blaxter 1986). However, experimental investigations combining the study of larval sensory system development and vulnerability to predation are limited. Larvae of several species, including the northern anchovy, *Engaulis mordax*, (O'Connell 1981; Webb 1981; Folkvord and Hunter 1986), Atlantic herring, *Clupea harengus harengus*, (Blaxter et al. 1983; Blaxter and Batty 1985; Fuiman 1989), Cape anchovy, *Engraulis capensis*, (Brownell 1985), bloater, *Coregonus hoyi*, (Rice et al. 1987), and white perch, *Morone americana*, (Margulies in press) have been studied to examine either sensory system development or predator-avoidance behaviors. Similar studies have been conducted on larvae of flatfish (Neave 1984, 1986) and several gadoids (Fridgeirsson 1978; Bailey 1984). These types of investigations, however, have not been combined during one study using a single cohort of experimental fishes.

The purpose of this study was to examine, experimentally, the size-specific vulnerability of white seabass, *Atractoscion nobilis*, larvae to different types of fish predators, and to determine if there was a developmental or neurological basis for any observed changes in larval vulnerability or behaviors. The developmental studies of larval white seabass centered on the ontogeny of two sensory systems, vision and

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mechanoreception, which are presumed to be important components of predator detection and larval escape responses (Blaxter 1986). The ontogeny of avoidance/escape responses and other larval behaviors of white seabass were then analyzed in relation to the structural and functional development of their sensory systems.

Very little is known of the early life history of the white seabass, even though it is the largest sciaenid occurring in coastal waters of California and Baja California and has historically been a favored sport and commercial species (Feder et al. 1974; Vojkovich and Reed 1983). White seabass spawn in spring and early summer in nearshore coastal waters of southern California, and produce pelagic eggs. Abundance and distribution of young-of-the-year in southern California waters have been reported by Allen and Franklin (1988). Larval morphological development has been described by Moser et al. (1983), but larval ecology, predator-avoidance behaviors, and sensory system development have not been described.

METHODS

Larval Rearing

White seabass larvae used in the experiments were hatched from eggs obtained from broodstock adults maintained at the Hubbs Marine Research Center at Sea World in San Diego. Eggs were transported to the aquarium at the Southwest Fisheries Center La Jolla Laboratory and stocked in 76 L aquaria at stocking densities of 6 L^{-1}. During the culture experiments water temperature ranged from 17° to 19°C, and a constant photoperiod of 13 h light: 11 h dark was maintained.

First-feeding white seabass larvae were fed rotifers, *Brachionus plicatilis*, cultured on the green alga *Tetraselmis*. Older larvae were sequentially fed diets of *Artemia* nauplii, a mixture of *Artemia* nauplii and wild copepods, and adult *Artemia*. The developmental size range of white seabass tested ranged from hatching (2.6 mm SL, 0 day after hatch) to juvenile metamorphosis (15.0 mm SL, 42 days after hatch) (Fig. 1).

Experimental Predators

Adult northern anchovy and juvenile white seabass were used as predators. Both of these predator groups occur in nearshore waters of southern California and are potential natural predators of white seabass larvae. These two predator groups represent different types of raptorial predatory behavior (Table 1). Adult northern anchovy are pelagic, cruising predators that attack prey at relatively high speeds and often from oblique angles. Juvenile white seabass attack at much slower speeds and have a somewhat discontinuous mode of attack that involves an approach, glide, and then engulfing of prey. Northern anchovy also initiate attacks from much greater distances.

Predators were held in laboratory holding tanks and fed adult *Artemia*, minced euphausiids and occasionally white seabass larvae. To minimize predator learning behavior, after completion of predation trials on a given date, predators were transferred to separate holding tanks; this ensured that no predator was used more than twice during the 6 wk experimental period.

Experimental Methods

The predation experiments were conducted following the methods of Folkvord and Hunter (1986), with several modifications. Predation trials were carried out in rectangular fiberglass tanks, 1.4 m^3 in volume, with a clear glass win-

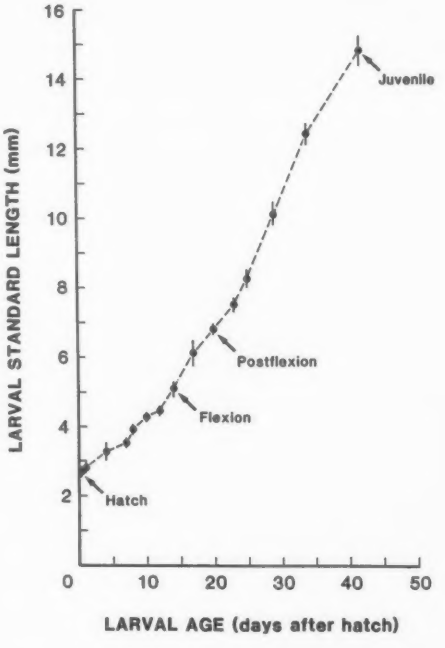

FIGURE 1.—Sizes, ages, and developmental stages of larval white seabass prey used in predation trials.

TABLE 1.—Modes of predation exhibited by adult *Engraulis mordax* and juvenile *Atractoscion nobilis*.

Predator	Size (mm)		Attack distance (dm)		Attack speed range (m/s)	Mode of attack
	Range	Mean	Range	Mean		
Engraulis mordax (Adults)	85–107	96.4	20–70	36.6	0.50–1.50	Fast speed; approach and attack continuous; often from oblique angle
Atractoscion nobilis (Juveniles)	62–86	72.2	5–30	14.7	0.05–0.20	Slow to moderate speed; attacks often discontinuous, with approach, glide, then ingestion; angle of attack horizontal or oblique

dow on one side for observation. Flourescent lamps produced 2,000–3,000 mc at the surface of each tank. A black plastic tent enclosed the window, providing a darkened compartment for observations. Metric rules placed on the tank window allowed estimation of predator attack distances. The tanks were supplied with flow-through ambient seawater (17°–19°C), except during an experiment when the water was static. Since adult northern anchovy often occur in large schools and juvenile white seabass are solitary or found in loose aggregations, it was decided that northern anchovy predators in groups of five individuals and white seabass in groups of three should be used. This simulated the predators' natural condition yet prevented predator "swamping" of larval prey.

Feeding motivation of predators was standardized by presenting constant numbers of adult *Artemia* to predators prior to predation trials with larvae. (*Artemia* are a good standard prey because they do not avoid predatory attacks by fishes.) Preliminary experiments had indicated that feeding behavior of adult northern anchovy was more variable than that of juvenile white seabass; thus, five groups of five *Artemia* each were presented to each anchovy predator group and three groups of five *Artemia* each were presented to white seabass. After the *Artemia* additions, white seabass larvae were introduced into the predation tanks in groups of five (each larval group added = trial). Trial duration was 10 minutes or until all prey were eaten. Larvae and *Artemia* were added to the tanks in clear beakers that were gently submerged at the water surface. After the initial *Artemia* trials, each predator group was tested with 6–8 larval trials, followed by a final *Artemia* trial to test for predator satiation.

On the same day as predation experiments, subsets of 10–12 larvae were removed from culture tanks and fixed in 5% formalin for calculation of mean larval sizes; additional subsets of larvae were removed for examination of sensory system ontogeny (discussed below). The total number of predator-prey interactions observed for each larval size class and predator type is presented in Table 2.

TABLE 2.—The total number of predator-prey interactions observed for each larval size and age class and predator type.

$\bar{x}$ larval size (mm)	Larval age (d)	Observations per predator type	
		Northern anchovy	White seabass
3.1	4	36	39
4.5	12	35	32
6.1	17	33	38
7.4	23	30	37
9.1	27	40	38
12.5	34	38	40
14.8	42	42	50

Classification of behaviors followed Folkvord and Hunter (1986). Four measures of predator-prey interactions were calculated: mean and maximum attack distances; percentage of larval avoidance responses; percentage of larval escapes; and predation rate (percentage of larvae captured during each 10 min trial). Approximate predator attack speeds also were estimated. A predator attack was a directed movement toward a prey with the mouth open. Predator attack distance was the distance in decimeters (dm) from a prey to the point of origin of attack. An avoidance response was a change in speed or direction of a larva occurring before a predator could complete an attack. An escape occurred when a predator failed to capture a larva during a single attack. Repeated attacks were scored as separate events.

Two potential biases to the predator-prey

interactions were addressed. Variation in predator performance was examined by calculating the percentage of predator error occurring in five groups of both types of predator feeding on adult *Artemia*. Since *Artemia* show no avoidance responses, a predator error was recorded when a predator simply missed the prey. Percentage of predator error was calculated for each predator group and among groups. In addition, potential stress or mortality of larvae due to handling was examined. For each larval size class, four replicates (trials) of five larvae each were transferred into 76 L tanks containing no predators. Mortality observed in control tanks was used to adjust for handling-induced mortality or increased vulnerability of larvae in predation trials.

Analysis of Larval Sensory System Development

Subsets of larvae from each size class were removed from culture tanks for analyses of larval visual and mechanoreceptive systems. Groups of 6–8 larvae from each size class were fixed in 5% phosphate-buffered formalin for histological analysis of organogenesis. Larvae were dehydrated, cleared, embedded in paraplast, and serially sectioned at 5 μm transversely and sagittally. Sections were stained with Harris' haemotoxylin, counterstained with eosin, and viewed under light microscopy at 80–1250 magnification. Ontogenetic development of the lens, retina, and optic tectum were examined and swimbladder inflation was noted. Size-specific visual acuity was calculated from retinal sections using the formula: $\sin \alpha = c/f$, where α is the minimum separable angle, c is the distance between the centers of adjacent cones, and f is the focal length of the lens (Neave 1984). Cones were measured as numbers per 100 μm length of retina (d), thus the reciprocal 10 d gives cone separation in mm. The expression was multiplied by 1.11 to adjust for approximate 10% shrinkage during processing, and the focal length of the lens was calculated by multiplying its radius (r) by 2.55 (Matthiessen's ratio; Matthiessen 1880), giving: $\sin \alpha = 0.0435/dr$.

Separate groups of 6–8 larvae from each size class were examined for development of free neuromast organs. These larvae were anaesthetized with MS-222 and immersed in a bath of the vital stain Janus Green (0.05% Janus Green made up with 50% seawater) (Blaxter et al. 1983). Larvae were immersed for 20–30 minutes and then removed for examination of number and location of free neuromasts under light microscopy.

Histological sections also were examined to determine the timing of swimbladder inflation in larvae.

Data Analysis

For each predation trial, predation rate (percent killed in 10 minutes) was calculated from the equation: $A = m + n - mn$, where A = total mortality rate, m = control mortality rate, n = experimental predation rate, and mn = the interaction effect which estimates the proportion of larvae consumed but which would have died anyway from handling stress or other causes (Ricker 1975). Percentage of larvae responding and escaping were considered total survival rates (S) and were calculated by first estimating total conditional mortality (A) (proportion "not responding" or "not escaping") and then calculating the difference as $S = 1 - A$ (Ricker 1975).

Lens diameter, visual acuity, and thickness of the optic tectum were calculated for each larval size class and developmental stage. Developmental ontogeny of the retina, optic tectum, and swimbladder were described. The mean number of neuromast organs also was calculated, and composite maps were developed of the patterns of neuromast organ formation.

Statistical analyses of data were performed using SAS (SAS 1982) statistical programs.

RESULTS

Predator/Prey Interactions

Potential Biases

Preliminary determinations of predator error by both predator types indicated that predator performance would not bias results. Mean predator error per trial for northern anchovy adults feeding on *Artemia* was 3.3% (range 2.1–5.1%) while error rate for juvenile white seabass was 2.7% (range 0.8–6.1%). There were no significant differences in mean error rate among predator groups, within trials, or between species (ANOVA, $P > 0.10$).

Larval mortality in control tanks (no predators) was low, ranging from 0.0 to 12.5% mean values for any larval size group. Experimental predation and escape rates were adjusted by the control rates.

Larval Responses

The probability of a white seabass larva responding to or escaping a predatory attack generally increased with larval size, although major differences in these responses were apparent depending upon type of fish predator. The mean percentage of larvae escaping attacks by northern anchovy ranged from 3% in yolk-sac larvae (3 mm SL) to 43% in metamorphosing fishes (15 mm SL) (Fig. 2A), while the percentage responding to anchovy attacks ranged from 14% (yolk-sac stage) to 56% (at metamorphosis) (Fig. 2B). Mean predation rate (percentage of larvae eaten in 10 minutes) by anchovy predators decreased from 95% on yolk-sac larvae to 56% on early juveniles (Fig. 2A). The predator/prey interactions were best described by exponential regressions (Fig. 2).

White seabass larvae were better able to respond to or escape attacks of juvenile white seabass than those of northern anchovy. Mean percentage of larvae escaping white seabass attacks ranged from 8% for yolk-sac larvae to 74% for metamorphosing fishes (Fig. 3A), while the percentage responding to attacks increased from 18% (yolk-sac stage) to 84% (at metamorphosis) (Fig. 3B). Responses and escapes from juvenile white seabass improved significantly in larger larvae, particularly between the larval sizes of 7.5 versus 9.0 mm SL (t-test, $P < 0.01$). Response and escape success nearly doubled during this developmental stage. Mean predation rate by juvenile white seabass predators decreased from 80% on yolk-sac larvae to 65% on 6 mm larvae, increased to 87% on 7.5 mm larvae, and then steadily decreased to 30% on early juveniles (Fig. 3A). These predation functions also were fit to exponential regressions (Fig. 3).

The success of avoidance movements by responding larvae (numbers escaping/numbers responding) generally increased with larval size (Table 3). Approximately 21% of responding larvae in the 3.1 mm size category successfully escaped northern anchovy attacks; this percentage increased to 50% in 4.5 mm larvae and 75% at metamorphosis. Avoidance success from juvenile white seabass attacks ranged from 39% for 3.1 mm larvae to 75% for 7.0 mm individuals and improved to nearly 90% in early juveniles.

Statistical comparison of the responses and escapes from northern anchovy versus white seabass predators indicated that a significantly higher percentage of larvae >6.0 mm SL

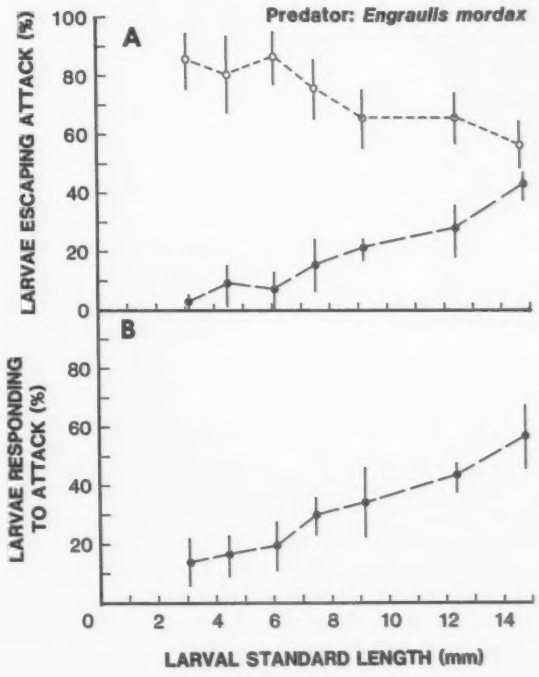

FIGURE 2.—Vulnerability of white seabass larvae to adult northern anchovy predators as a function of larval length. A. Solid circles are percentage of larvae escaping an attack, error bars are 2 × SE, regression equation is Arcsine $Y = 5.078\ e^{0.144SL}$ ($n = 44$, $r^2 = 0.73$), where Y = proportion of larvae escaping and SL = larval standard length (mm); open circles are percentage of larvae eaten in 10 min trials, error bars are 2 × SE, regression equation is Arcsine $Y = 81.326\ e^{-0.035SL}$ ($n = 44$, $r^2 = 0.96$), where Y = proportion of larvae eaten in 10 minutes and SL = larval standard length (mm). B. Percentage of larvae responding to an attack, error bars are 2 × SE, regression equation is Arcsine $Y = 15.293\ e^{0.081SL}$ ($n = 44$, $r^2 = 0.89$), where Y = proportion of larvae responding and SL = larval standard length (mm).

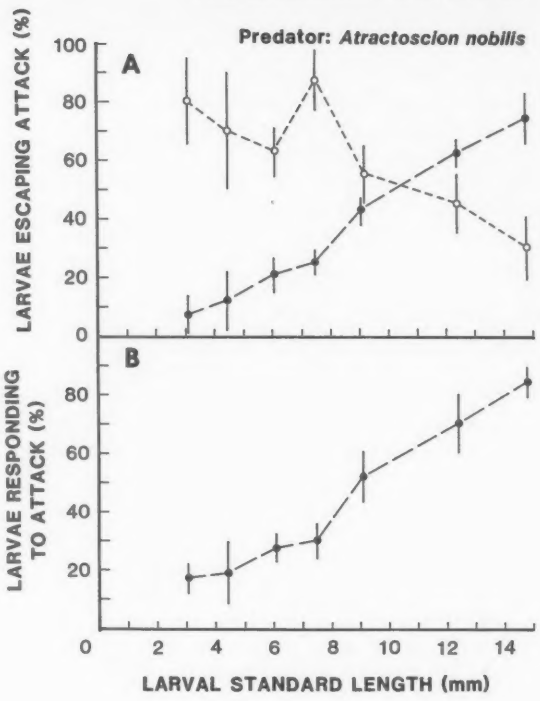

FIGURE 3.—Vulnerability of white seabass larvae to juvenile white seabass predators as a function of larval length. A. Solid circles are percentage of larvae escaping an attack, error bars are 2 × SE, regression equation is Arcsine $Y = 10.976\ e^{0.120SL}$ ($n = 44$, $r^2 = 0.89$), where Y = proportion of larvae escaping and SL = larval standard length (mm); open circles are percentage of larvae eaten in 10 min trials, error bars are 2 × SE, regression equation is Arcsine $Y = 81.210\ e^{-0.048SL}$ ($n = 44$, $r^2 = 0.92$), where Y = proportion of larvae eaten in 10 minutes and SL = larval standard length (mm). B. Percentage of larvae responding to an attack, error bars are 2 × SE, regression equation is Arcsine $Y = 16.822\ e^{0.096SL}$ ($n = 44$, $r^2 = 0.94$), where Y = proportion of larvae responding and SL = larval standard length (mm).

TABLE 3.—Avoidance success of responding larvae (numbers escaping/numbers responding).

	Predator type			
	Northern anchovy		White seabass	
Larval SL (mm)	$\bar{x}$ escape success	SE	$\bar{x}$ escape success	SE
3.2	21.4	4.9	38.8	7.1
4.3	47.0	11.5	57.9	9.1
6.8	63.0	13.2	70.0	7.0
7.4	51.7	6.7	80.0	7.5
9.2	58.8	7.3	81.1	6.6
12.4	64.3	5.3	90.0	5.1
14.8	75.0	6.0	88.0	4.5

escaped white seabass attacks, while a significantly higher percentage of larvae >7.5 mm SL responded to white seabass attacks (ANCOVA with Least Squares Means, $P < 0.05$). This increased responsiveness to white seabass predators (compared to northern anchovy) translated into significantly reduced consumption rates by white seabass predators on larvae >8.5 mm SL (ANCOVA with Least Squares Means, $P < 0.05$).

Larval Visual Ontogeny

The Retina and Visual Acuity

Histological examination of the white seabass visual system revealed numerous developmental changes from hatch to juvenile metamorphosis. In yolk-sac larvae, the lens was present, but the retina was unpigmented and undifferentiated. At time of yolk absorption (ca. 3.2 mm SL), the retina became differentiated into distinct layers, the photoreceptive layer contained visual cells and the epithelial (basal) layer became pigmented. Presumably, at this stage the eye was functional.

In young larvae (3.5–7.0 mm SL), the retina appeared to be composed of only cone cells and no retinomotor (light-dark) responses were noted by either the photoreceptor cells or the epithelial masking pigment. In larvae >4 mm SL, the posteroventral area of the retina (~15–20° below the horizontal plane) was characterized by densely packed cone cells, constituting an *area temporalis*. A lens retractor muscle first appeared histologically at a standard length of 4.5 mm (Fig. 4). Seen in sagittal section, the lens retractor articulated posteriad with the ventral

floor of the retina and anteriad to the lens by means of an extremely thin ligament. In older larvae and juveniles, the lens retractor became bipartite, presumably aiding in movements of the lens posteriad and/or ventrad.

The outer nuclear layer (ONL) of the retina, containing the photoreceptive cell nucleii, was single-tiered until larvae reached a length of 7.0–7.5 mm SL. At this stage, compact and darkly staining mitotic bodies began to appear in the ONL (Figs. 5, 6A); these mitotic bodies appeared to be rod precursors. At a larval length of 10.5 mm SL, double cones were present in the photoreceptive layer and the ONL was multitiered. At 12.5 mm SL the ONL nucleii were multilayered and a clear retinomotor response was evident, indicating the presence of rods (Figs. 6A, 7).

During ontogeny the density of cone cells in the photoreceptive layer decreased linearly, while lens diameter increased linearly (Fig. 6B). Visual acuity improved nonlinearly with larval size, changing from 91 minutes of arc in first-feeding larvae to 26 minutes in metamorphosing fishes (Fig. 6A). The period of most rapid improvement in acuity occurred from approximately 4–9 mm larval length.

Development of the Optic Tectum

In yolk-sac larvae, the optic tectum of the mesencephalon (midbrain) was composed of undifferentiated matrix cells. During early feeding stages, the tectum differentiated into an inner, neuronal *stratum periventriculare* (SPV) and an outer, fibrous *stratum zonale* (SZ) (Fig. 8). This bilayered configuration persisted throughout the larval stages, with the entire tectum and the outer SZ thickening during ontogeny (Fig. 9A, B). The period of most rapid tectal differentiation during the early life stages occurred from approximately 3 to 9 mm larval

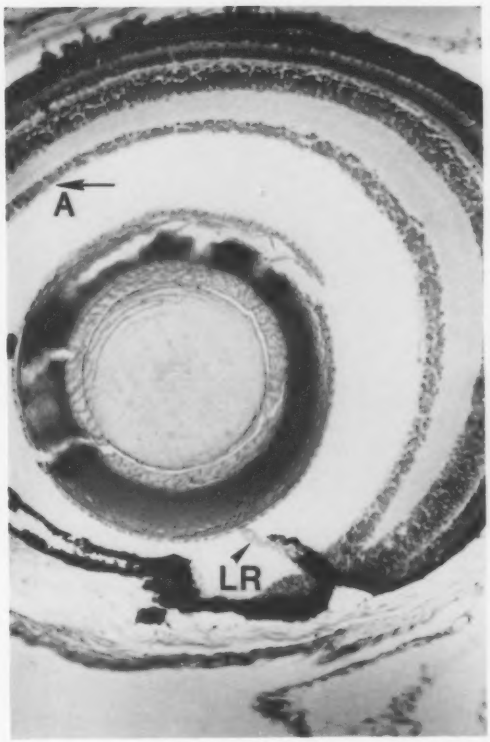

FIGURE 4.—Sagittal section of the eye of a 4.8 mm SL white seabass larva showing the position of the lens retractor muscle (LR). (A) indicates the anterior direction. ×100.

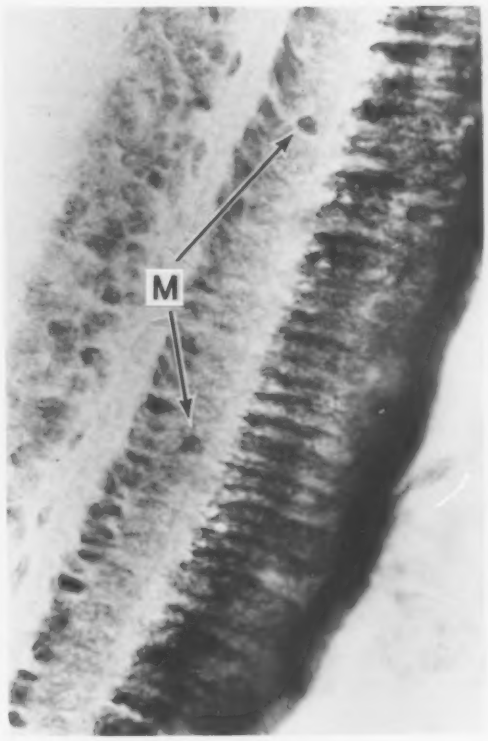

FIGURE 5.—Cross-section of the retina of an 8.0 mm SL white seabass larva showing several dark mitotic bodies (M) in the outer nuclear layer. ×250.

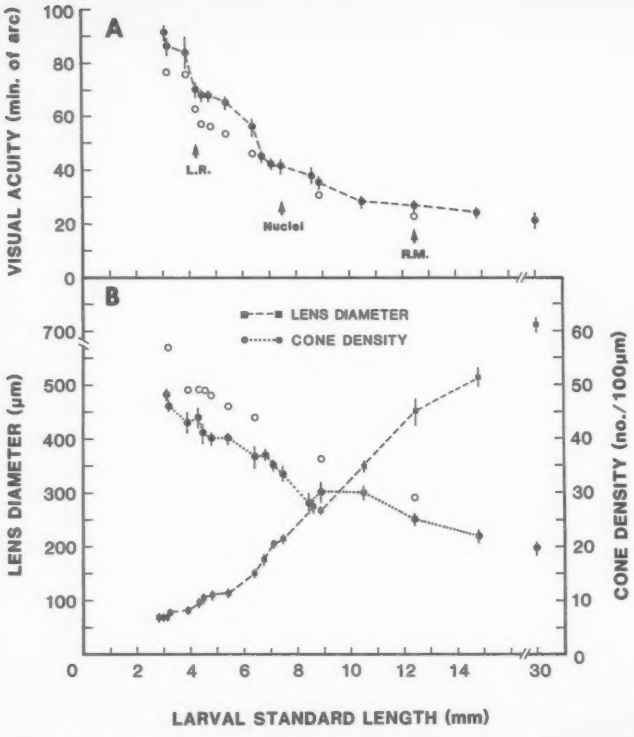

FIGURE 6.—Visual development of larval white seabass as a function of larval length. A. Visual acuity, error bars are 2 × SE, regression equation is $Y = 138 - 18.2\ SL + 0.726\ SL^2$ ($n = 66$, $r^2 = 0.96$), where Y = visual acuity (min of arc) and SL = larval standard length (mm). L.R. is the first appearance of the lens retractor muscle; Nuclei is the first appearance of mitotic bodies in the outer nuclear layer; and R.M. is retinomotor response. B. Squares are changes in lens diameter, error bars are 2 × SE, regression equation is $Y = -58.7 + 37.8\ SL$ ($n = 78$, $r^2 = 0.97$), where Y = lens diameter (µm) and SL = larval standard length (mm); circles are changes in cone cell density, error bars are 2 × SE, regression equation is $Y = 52.6 - 2.3\ SL$ ($n = 66$, $r^2 = 0.89$), where Y = cone cell density (no./100 µm) and SL = larval standard length (mm). Open circles are measurements taken in the *area temporalis*. Values for a 30 mm SL juvenile are given for comparison to larvae.

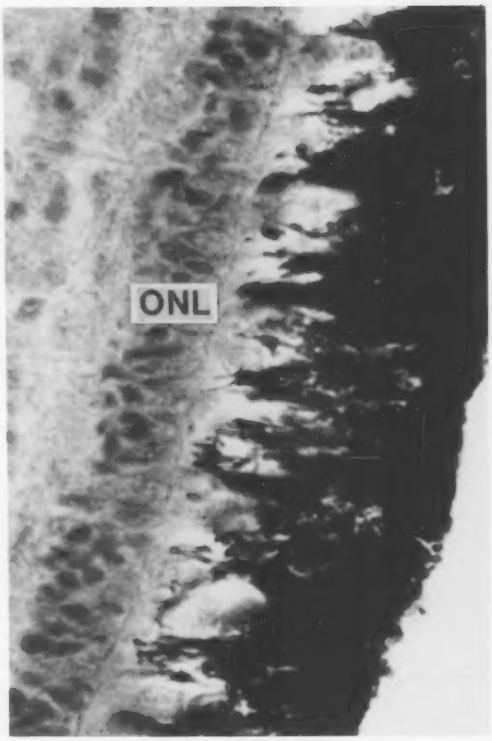

FIGURE 7.—Retinomotor response of a 12.5 mm SL, light-adapted white seabass larva, showing migration of the epithelial masking pigment. ONL is the outer nuclear layer. ×400.

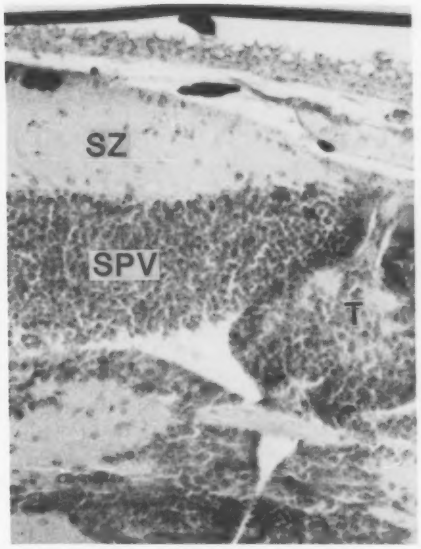

FIGURE 8.—Cross-section through the optic tectum of a 9.2 mm SL white seabass larva. The tectum is bilayered at this stage, with an inner *stratum periventriculare* (SPV) and an outer *stratum zonale* (SZ). The SZ is thickening and exhibits increasing numbers of neurons migrating from the inner layer. The *torus longitudinalis* (T) is quite prominent by this stage. ×100.

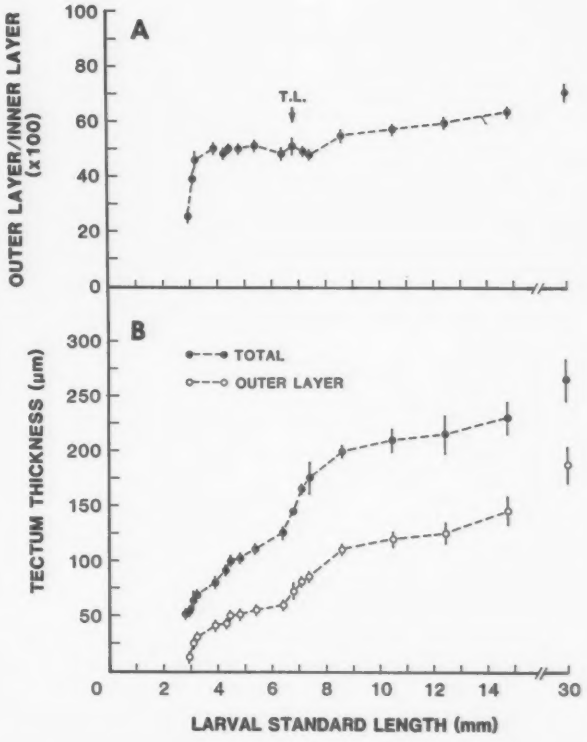

FIGURE 9.—Development of the optic tectum of larval white seabass as a function of larval length. A. Change in the ratio of the outer layer/inner layer, T.L. is the first appearance of the *torus longitudinalis*. B. Solid circles represent total thickness of tectum, error bars are 2 × SE, regression equation is $Y = -48.6 + 38.8\ SL - 1.35\ SL^2$ ($n = 64$, $r^2 = 0.97$), where Y = total width of tectum (μm) and SL = larval standard length (mm); open circles represent thickness of outer layer, error bars are 2 × SE, regression equation is $Y = -33.8 + 20.3\ SL - 0.56\ SL^2$ ($n = 60$, $r^2 = 0.97$), where Y = width of outer layer (μm) and SL = larval standard length (mm). Values for a 30 mm SL juvenile are given for comparison to larvae.

length (Fig. 9B). Growth and differentiation of the SZ appeared to involve cell migrations from the inner SPV with a progressive increase in the SZ:SPV ratio (Fig. 9A). This ratio increased rapidly at first feeding (~3–4 mm SL), stayed constant at lengths of 4.0–7.5 mm SL, and then increased again from 7.5 mm to early juvenile stages.

Another important event in the ontogeny of the optic tectum involved the development of the *torus longitudinalis* (TL). This structure first appeared histologically at a larval length of 6.8–7.0 mm SL (Fig. 9A). Seen in transverse section, the TL developed as a teardrop-shaped structure with a wide area of contact dorsad with the optic tectum and ventrad with the epithalamus (Fig. 8). The TL continued to grow with ontogeny, and in older larvae and early juveniles the TL exhibited an increasing number of neuronal projections to the cerebellum.

Ontogeny of Mechanoreceptors

Neuromast Development

Staining with Janus Green provided somewhat variable results, in that not all white seabass larvae took up the stain equally well. Some neuromast organs stained better than others, but the use of 6–8 fish per larval size class seemed to provide good composite patterns of neuromast formation.

At hatching, larvae had 5 or 6 pairs of neuromasts on the head and 5 or 6 pairs extending along the trunk (Fig. 10A, B). All of these organs appeared to be free neuromasts (not enclosed by canals). Each free neuromast consisted of a basal, naked neuromast organ attached apically to a cylindrical, gelatinous cupula. The only other stained structures were the nasal pits.

The total number and patterned formations of free neuromasts increased with ontogenetic development (Figs. 10, 11). At first feeding, larvae had 6–8 neuromasts on the head and 6 or 7 on the trunk. During development, new head neuromasts appeared first in the supraorbital and infraorbital areas, while on the trunk they recruited midlaterally (Fig. 11). The period of most rapid addition of free neuromasts was in the larval size range of 4–9 mm SL. During the early postflexion stage (~7–10 mm SL), free neuromasts began to form in distinct supraorbital, infraorbital, and preopercular (hyomandibular) rows on the head and in a single midlateral row on the trunk (Figs. 10, 11). By 12.5 mm SL,

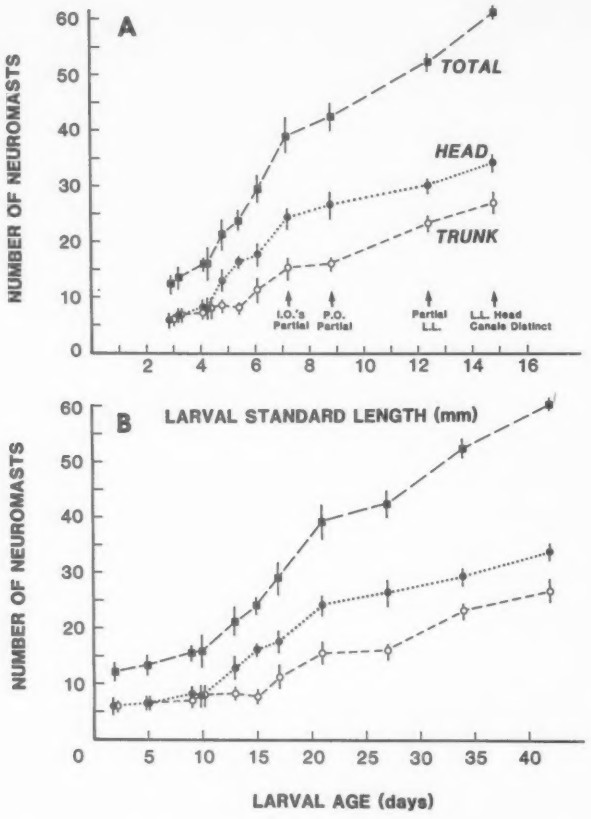

FIGURE 10.—Numbers of free neuromasts developing on larval white seabass as a function of larval length (A) and age (B). Error bars are 2 × SE. I.O.'s are infraorbital and supraorbital rows on the head; P.O. is the preopercular or hyomandibular row on the head; and L.L. is the lateral line. Values are based on staining and should be considered approximate only.

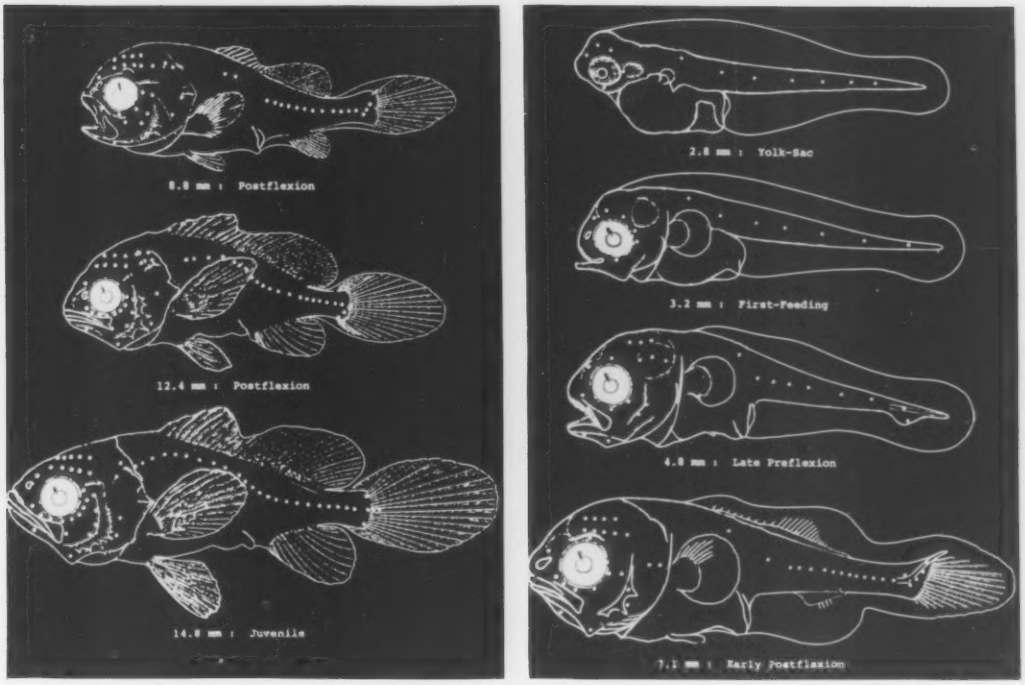
8.8 mm : Postflexion
12.4 mm : Postflexion
14.8 mm : Juvenile
2.8 mm : Yolk-Sac
3.2 mm : First-Feeding
4.8 mm : Late Preflexion
7.1 mm : Early Postflexion

FIGURE 11.—Composite maps showing the location of free neuromast organs during development of white seabass larvae. Larval outlines were modified from those of Moser et al. (1983).

some of the recruiting neuromasts were being enclosed by canals on the head and trunk; some existing free neuromasts were being incorporated in canals as well. At juvenile metamorphosis, the three major branches of the head canals, as well as the lateral line on the trunk, were fairly distinct (Figs. 10A, 11), forming the precursor to the juvenile and adult lateral line system.

Swimbladder Development

In yolk-sac larvae, the swimbladder appeared as a collapsed sac dorsad to the yolk sac, while in first-feeding larvae it was still partially flattened and situated dorsad to the anterior digestive tract. Timing of complete swimbladder inflation was variable; most larvae exhibited full inflation at lengths of 4.5–5.5 mm SL. In larvae >4 mm, a pneumatic duct was present in the anterodorsal area of the swimbladder. It was not clear whether swimbladder inflation occurred by way of air-gulping at the surface or by gas secretion internally.

DISCUSSION

Neurosensory Basis For Avoidance Responses

The overall probability of white seabass larvae escaping predatory attacks seems highly dependent on the size of the larvae, the type and quality of sensory input being integrated by the larvae, and the type of predator encountered (Fig. 12). Yolk-sac larvae have nonfunctional eyes, a small number of free neuromast organs on the head and trunk, and a noninflated swimbladder. At first feeding (~3.2 mm SL), the eye becomes functional, but visual acuity is poor; the pure-cone retina limits peripheral vision and motion detection, and no accommodation is possible (since there is no lens retractor muscle). There is strong correlative evidence that increases in numbers of free neuromasts and improvements in the visual system are responsible for the improved avoidance responses observed in predation trials. In larvae <4.5 mm SL, predator detection is most likely a function of mechanoreception by free neuromasts, since visual

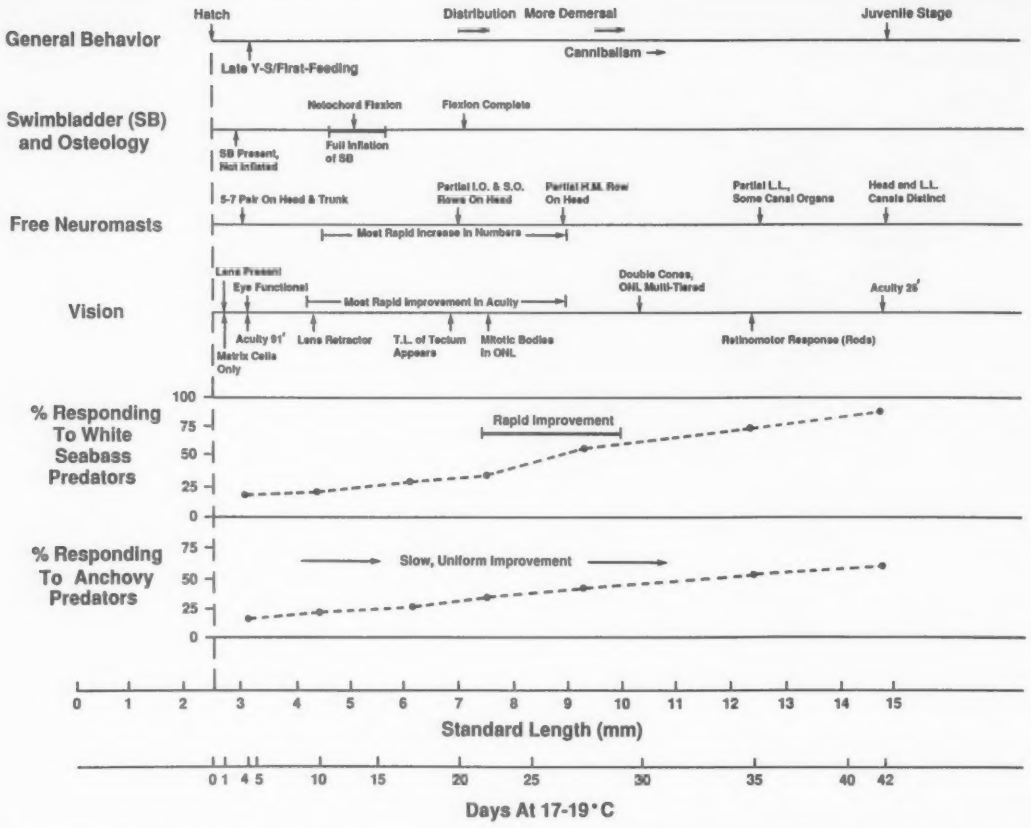

FIGURE 12.—Developmental events and sensory system development during the early life history of the white seabass. Format is based on Hunter and Coyne (1982). Developmental data are from my study, except some behavioral data from Orhun (unpubl. data) and osteological data from Moser et al. (1983). Y-S = yolk-sac stage, I.O. = infraorbital, S.O. = supraorbital, H.M. = hyomandibular, L.L. = lateral line, T.L. = *torus longitudinalis*, ONL = outer nuclear layer of retina.

acuity is poor and no acoustic inputs are likely through the swimbladder. During notochord flexion (~5–7 mm SL), visual accommodation is developed with the lens retractor muscle, the swimbladder is inflated (potentially providing acoustic stimuli), and there begins a major recruitment of free neuromasts on the head and trunk. Up to this point in development, it would appear that vision plays a limited role in predator detection.

During the early postflexion stage (~7 mm), the visual system begins to undergo numerous changes (Fig. 12). Acuity continues to improve, early rod precursors develop in the retina, the optic tectum increases markedly in size and stratification, and the *torus longitudinalis* begins to develop in the midbrain. At 10.5–12.5 mm SL, double cones and early rod cells are present in the retina. These changes are essential to visual improvement and integration. Visual acuity calculated for most adult marine fishes is 2–10 minutes of arc (Tamura 1957); values for adult white seabass are unknown but probably fall in this range. Thus, approximately 75–80% of the improvement in acuity seen from hatch to adult stage in white seabass has occurred by the late larval stage. However, for vision to play a major role in predator detection, improvement in acuity must be accompanied by development of rod cells, by accommodation to distant objects (lens retractor muscle), and by growth and development of the optic tectum. The development of rod vision helps to improve peripheral vision (O'Connell 1981) and motion detection (Blaxter 1986), both crucial aspects of predator detection. Rods also aid in improved visual performance in dimmer light (O'Connell 1981), which would improve foraging skills and predator-detection

as white seabass become more demersal. Growth and stratification of the optic tectum allow for more complex interconnections with other brain centers in teleosts and are essential for the development of progressively more sophisticated behavioral responses (Munro 1984). The *torus longitudinalis* functions in midbrain integration of proprioceptive information (Groman 1982) and is involved in the control of visual motor patterns (Munro 1984).

The free neuromasts in fish larvae probably function in detection of differences in velocity between the fish and surrounding water. The incorporation of neuromasts into canals (as occurs in older white seabass larvae and early juveniles) probably aids in schooling or detection of accelerations in water movements caused by other animals, such as predators (Blaxter et al. 1983). The increases in numbers and in patterned formations of neuromasts with white seabass larval size probably improve detection of predator movements and aid in swimming movements and proprioception.

During the early postflexion stage (7.5–10.0 mm SL), these improvements in mechanoreceptive and visual capabilities appear to be directly related to improved detection and escape responses. However, depending upon the type of predator encountered, a significant difference exists in the degree of improvement in avoidance capabilities (Fig. 12). Early postflexion larvae exhibit a modest improvement in evading northern anchovy attacks, but display a dramatic improvement in detecting and escaping the slower, more discontinuous attacks of juvenile white seabass. Since some startle responses are elicited even in yolk-sac larvae, it appears that neural motor pathways such as Mauthner-type neurons (Eaton and DiDomenico 1986) are present and functioning during all developmental stages. Just prior to and during the early postflexion stage, larvae undergo notable additions of neuromast organs and major improvements in the visual system. Since the outcome of a predator-prey interaction is heavily dependent upon reaction velocity and timing (Webb 1976), the slower, close-range attacks of juvenile white seabass probably allow more time for detection of sensory stimuli from several modalities as well as sensory-motor integration needed for response and escape movements.

Improvements in visual and mechanoreceptive systems have been implicated in the evasion behaviors of northern anchovy larvae (Webb 1981; Folkvord and Hunter 1986), while acoustic stimuli detected through the gas-filled otic bullae seem important in the development of startle responses of Atlantic herring larvae (Fuiman 1989). The inflation of the otic bullae with gas and the occurrence of a well-developed acoustico-lateralis system, however, seems to be more characteristic of clupeoid larvae (Fuiman 1989). Although acoustic stimuli or Rohon-Beard (mechanoreceptive) input could also be related to improved evasion responses of white seabass larvae, the observed improvements in the neuromast and visual systems seem to be directly related to the improved avoidance capabilities.

Larval Vulnerability to Attacks

Larval size and developmental stage are the most important factors related to larval vulnerability in laboratory trials. The type of predator encountered also influences predation rates. However, although white seabass larvae were better able to respond to juvenile white seabass attacks than those of northern anchovy, this did not result in significantly reduced predation rates (in comparisons between predator types) until larvae were >8.5 mm in length. This suggests that other factors related to predator detection of prey, such as prey morphology, water clarity, and alternative prey abundance, may be as important as predator type in controlling vulnerability of small white seabass larvae. Physical background and morphological conspicuousness of prey can be important factors controlling predation rates of planktivorous fishes (Vinyard and O'Brien 1976), while relative abundance of alternative prey has been shown to have significant effects on fish consumption rates on small white perch larvae (Margulies in press).

One disadvantage of laboratory studies is that realistic encounter rates between larval prey and fish predators are difficult to simulate. Although the main purpose of this study was to delineate the developmental basis for larval avoidance behaviors, it is important to recognize the limitation of predicting total vulnerability of larvae based on laboratory trials only. Total vulnerability to predation is a function of the probability of encounters between predator and prey, the probability of capture of prey and the probability of attacks by a predator (O'Brien 1979). My data provide reliable estimates of probability of prey capture and, to a lesser degree, probability of attacks by the experimental fish predators. Encounter rates, however, are affected by a

number of larval growth-related parameters, including increased larval swimming speeds and search volumes and increased conspicuousness of larger larvae (Hunter 1981). It is possible that increasing encounter rates between a suite of predators and larger white seabass larvae in natural systems would offset the observed steady increase in detection and escape responses observed in larger larvae in laboratory trials. This could occur until larvae became invulnerable to attacks. My laboratory data provide some hint of this pattern in the slightly increased predation rates on larvae in the 4.5–7.5 mm size range (see Figures 2A, 3A). However, white seabass larvae are relatively inactive and become increasingly demersal during ontogeny, thus, they might not be subject to significantly higher encounter rates with predators. This remains speculative, however, and is an area for future investigation.

Implications for White Seabass Early Life History

Compared with white seabass larvae, California sardine, *Sardinops sagax*, and northern anchovy larvae (co-occurring pelagic larvae in nearshore southern California waters) appear better able to detect and avoid attacks by adult northern anchovy predators at comparable stages of larval development (Folkvord and Hunter 1986; Butler and Pickett 1988). These two clupeoid species also exhibit schooling behavior in the later larval stages. Many species exhibit a combination of larval adaptations to minimize fish predation, including long periods of transparency (e.g., dover sole, *Microstomus pacificus*; Hunter[1]), rapid development of avoidance capabilities (northern anchovy and sardine) and schooling (clupeoids). During early feeding stages, white seabass larvae develop a robust, highly pigmented body form and exhibit limited mobility. During the early postflexion stage (7–10 mm), white seabass start to abandon a strictly pelagic distribution and become noticeably more demersal. By the late larval and early juvenile stage, they are found almost exclusively associated with submerged cover (often drift algae) or near-bottom habitats (pers. obs.; Allen and Franklin 1988; Orhun[2]; Kramer[3]). In nearshore waters of southern California, other sciaenid larvae show a marked vertical size distribution during daylight hours, with larger larvae (postflexion and larger) occurring in highest densities in suprabenthic habitats and smaller larvae occurring higher in the water column (Love et al. 1984; Jahn and Lavenberg 1986). The suprabenthic distribution of larger larvae has been characterized as a possible adaptation to high concentrations of food, for predator-avoidance or for maintenance of position on the continental shelf. However, recent studies of white croaker, *Genyomenus lineatus*, larvae indicate that the suprabenthic distribution of older sciaenid larvae is probably not related to feeding (Jahn et al. 1988).

My results indicate that this ontogenetic shift deeper into the water column by older white seabass larvae (and other sciaenids) may be related to their predator-avoidance capabilities. The dominant planktivorous species encountered in midwater habitats of nearshore southern California waters are fast-swimming, shoaling pelagics such as northern anchovy, sardine, and Pacific mackerel, *Scomber japonicus*. Potential planktivores in near-bottom habitats include sciaenids, gobiids, embiotocids, clinids, serranids, and various flatfishes (Eschmeyer et al. 1983). All of these demersal species exhibit some type of ambush, hovering, discontinuous, or close-range mode of predatory behavior, similar to the attack behavior of juvenile white seabass, and all attack at slower speeds than the shoaling pelagics. Based on my experimental evidence, it is likely that, as they drop out of the plankton, older white seabass larvae maximize their predator-detection and avoidance capabilities when encountering demersal predators. Remaining in the plankton in later larval stages and being exposed to pelagic, shoaling fish predators would prolong a period of extreme vulnerability, while shifting to a demersal distribution would place white seabass in habitats to which they are better suited developmentally.

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Residence Times, Distribution, and Production of Juvenile Chum Salmon, *Oncorhynchus keta*, in Netarts Bay, Oregon

William G. Pearcy, Christopher D. Wilson, Alton W. Chung, and John W. Chapman

ABSTRACT: Juvenile chum salmon resided in Netarts Bay, a small, shallow estuary at the southern spawning range of chum salmon in the Northeast Pacific, from mid-March until June during each of three years from 1984 to 1986. Early in the spring they were most abundant in beach seine catches during high tide in the upper bay, indicating extensive intertidal excursions. Later in the spring, when temperatures exceeded 14°–16°C in the upper bay, they were most common in catches at low tide in the lower bay. Based on recaptures of fin-clipped hatchery fish, the residence of juveniles varied inversely with size of fish at release. Large (6.5 g) fish immediately emigrated from the estuary and 3–4 times as many returned as adult fish as 1.0 and 2.2 g juveniles, which had residence half-lives of 5–16 days. Growth rates of juvenile chum salmon during the 3 years were similar, but were low (1.6–2.3% body weight/day) compared with other studies. Production was also low. This may be related to high metabolic costs at above optimal temperatures and the large size of available prey in Netarts Bay.

The period of early marine residence is thought to be a critical stage in the life history of Pacific salmon, affecting the survival of young and the numbers of adults returning in subsequent years (Parker 1968; Peterman 1978; Pearcy 1984). The period of estuarine residence may be especially important for chum salmon, *Oncorhynchus keta*, (Healey 1982a; Simenstad and Wissmar 1984). They enter estuaries at a small size and presumably need to grow rapidly to avoid intense predation after they enter the ocean (Parker 1971; Simenstad and Salo 1980; Healey 1982b; Simenstad and Wissmar 1984). The capacity of an estuary to produce salmon may be limited, however, and the availability of prey resources may affect salmon emigration, growth, ability to avoid predation, and thus survival (Reimers 1973 Bailey et al. 1975; Healey 1979, 1980a; Sibert 1979; Simenstad and Salo 1980).

The hypothesis that the estuarine phase of the early life history of chum salmon is critical needs to be tested (Simenstad and Wissmar 1984; Levings 1984). If this phase is essential, increased releases of hatchery fish from private or public hatcheries may not be beneficial unless release strategies minimize or circumvent density-dependent growth and survival in estuaries, e.g., by modifying size, time, or numbers of fish released. Healey (1979, 1982a) concluded that seaward migration was size dependent, and Ioka (1978, unpubl. data) reported that large (>8 g) juvenile chum salmon were capable of migrating directly into offshore waters. This suggests that estuarine rearing may not be essential for chum salmon released from hatcheries at a large size.

To evaluate the capacity of estuaries to produce chum salmon, we studied their downstream movement, distribution, abundance, residence time, growth, and production in Netarts Bay, OR. Netarts Bay is a small estuary along the northern Oregon coast, near the southern distribution of chum salmon along the coast of the northeastern Pacific Ocean (Henry 1953). Netarts Bay was selected for this study because the Oregon State University chum salmon hatchery (Lannan 1975, 1983) enabled experimental releases of chum salmon at different times and sizes, and because the residence times and growth of chum salmon in a small estuary needed to be compared with the results found in estuaries farther north.

Netarts Bay (Fig. 1), located along the northern Oregon coast, has an area of only 10 km^2 at mean high water (MHW). The bay is strongly influenced by the ocean. Salinities generally approach ocean levels. The intertidal volume is about 75% of the volume at MHW; 12% of the Netarts Bay is subtidal (Glanzman et al. 1971;

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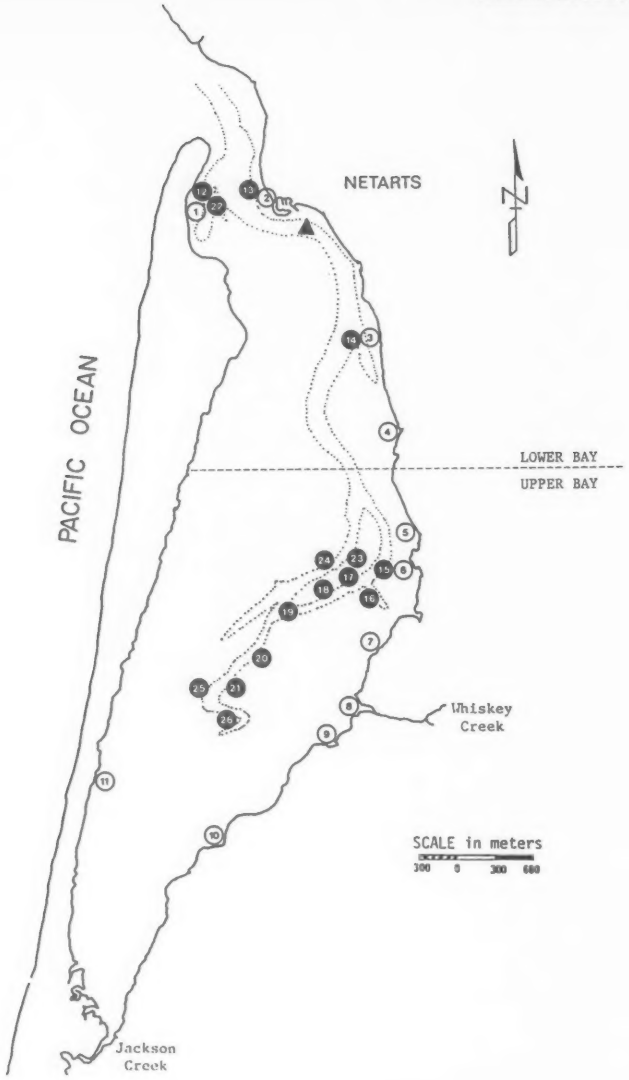

FIGURE 1.—Netarts Bay with locations of high tide (open) and low tide (solid) seine stations and the tow net stations (triangle).

Kreag 1979). The watershed area is small (about 36 km^2), and its only tributaries are small creeks. Whiskey Creek, the site of the Oregon State University experimental hatchery for rearing chum salmon (Lannan 1975), and Jackson Creek are the two largest streams that drain into Netarts Bay and are the major spawning habitats for chum salmon in Netarts Bay. Besides cutthroat trout, only a few rainbow (steelhead) trout and coho salmon were found in Whiskey or Jackson Creek.

METHODS

The contribution of naturally spawned chum fry to Netarts Bay and the timing of their outmigration were estimated from samples of chum salmon fry captured in a fyke net, located in Whiskey Creek about 100 m from the bay at MHW, from late March to early May 1984, and from late February through late May 1985 and 1986. The net, which was used for 35, 51, and 53 days in 1984, 1985, and 1986, respectively, was

constructed of 3.2 mm mesh with a 1.3 m wide mouth opening and two 2.7 m wings. The net was positioned across 95% of the width of the stream except during periods of high stream flow (Wilson and Pearcy 1985a). Catches were monitored during day and night periods. The net was removed from the stream on a few occasions during daylight hours and periods of high stream flow. The sampling error resulting from removing the net during daylight hours is assumed to be minimal as <1% of the total number of chum fry were caught in the fyke net during these hours (Wilson and Pearcy 1985a). Outmigrating juvenile chum salmon were also sampled in Jackson Creek with a 3.2 mm mesh bag net stretched across this stream two nights per week between 19 March and 25 April 1986. Water depth, temperature, cloud cover, and flow rates (1986 only) were recorded from both Whiskey Creek and Jackson Creek during sampling periods. Juvenile chum salmon in the catches were counted and fork lengths (FL) were measured to the nearest 1 mm for all fish or for a subsample of 100 fish per sampling period.

Fin-clipped (ventral and adipose) chum salmon were released from the Whiskey Creek hatchery to estimate residence time and growth of fish entering the bay at different times and different sizes. Data on the releases of marked and unmarked fish are summarized in Table 1. Eggs from adult chum salmon returning to Whiskey Creek were reared at the hatchery and at the Oregon Aqua-Foods, Inc. (OAF) hatchery in Springfield, OR. OAF fish were returned to raceways and acclimated at the Whiskey Creek facility for 10–13 days before release into Netarts Bay. These OAF fish were smaller at release than fish reared at Whiskey Creek in 1984, but were larger than Whiskey Creek fish in 1986 (Table 1). Differential mortality of fin-clipped vs. unclipped fish was not evident for fish held 3–4 days after marking in 1984 and 1985, or for OAF fish marked 10–13 days before release in 1986.

Two problems affected releases of juvenile chum salmon from the Whiskey Creek facility. Some marked fish escaped from the raceway and were caught in the bay before their planned release on 16 April 1984. The second problem was a bacterial disease that afflicted many fish reared at the Whiskey Creek facility in April 1986. About 4.4% of the fish died during marking operations, and 7.7% of the fish that survived marking died after being held in the raceway for 24 hours. Thus the numbers of fish released on 28–29 April 1986 are overestimates of the numbers of healthy fish actually entering the Netarts Bay. The raceway was sterilized with formalin after this release, and no apparent adverse effects were observed on the OAF fish transported to the Whiskey Creek facility in May 1986.

Netarts Bay was sampled for juvenile chum salmon from mid-March through late June 1984 and 1986 and from late February through early

TABLE 1.—Summary of releases of marked and unmarked juvenile chum salmon from the Whiskey Creek hatchery in 1984, 1985, and 1986.

Date	Total no. released × 1000	× FL (mm)	× Wt. (g)	Marks	No. marked × 1,000	% marked
1984						
1 April	215.1–344.1	52	1.4	0		
16 April	516.2–645.2	58	1.9	RV	24.0	
16 April		46	[1]0.75	LV	[2]20.5	
Total	731.3–989.3				44.5	4.5–6.1
1985						
19 April	155.6	56	1.8	RV	18.2	
26 April	218.4	59	1.9	LV	20.2	
Total	374.0				38.4	10.3
1986						
28–29 April	609.0	48	0.97	RV	[3]14.7	
11 May	43.6	62	2.2	RV + A	[2]21.4	
11 May		92	6.5	LV + A	[2]22.2	
Total	652.6				58.3	8.9

[1]Measured on 3 April 1984.
[2]Oregon Aqua-Foods Inc. fish reared offsite.
[3]Estimated no. released after mortality.

July 1985. A 37 m long, tapered, floating beach seine, set in a semicircle from the shoreline from a 4.6 m boat with an 18 hp outboard motor, was used for sampling. Sets encompassed about 100 m^2. The seine had a maximum depth of 2.5 m in the bunt and 0.7 m at the ends of the wings. The wings were made of 2.5 cm (stretch) mesh and the bag was made of 0.64 cm mesh. We sampled 11 high tide stations (1–11) and 10 low tide stations (12–21) in 1984–85 and 11 high tide stations (1–11) and 8 low tide stations (12, 13, 14, 22–26) in 1986 (Fig. 1). (Specific beach seine stations are described by Wilson and Pearcy (1985a) and Chung and Pearcy (1986).) The numbers of beach seine hauls made in 1984, 1985, and 1986 were 435, 333, and 388, respectively. Surface water temperatures were measured to the nearest 0.1°C with a bucket thermometer, and surface salinities were determined to the nearest 2‰ with an American Optical Model 10419[1] refractometer after each set. Each station was sampled several times each month during the field seasons.

We used a Kvichak towed net[2] with a 2.7 × 2.7 m mouth opening and a 8.2 m long body section with mesh grading from 3.8 cm to 0.3 cm and a cod end of 0.3 cm mesh to sample juvenile chum salmon in the main tidal channel during slack tide at approximately 2 wk intervals from late March through late June 1985. One nighttime tow was made. Two boats were used to pull the net along a 900 m long transect in the main channel of the lower bay (Fig. 1) at speeds of about 1–2 m/s.

Approximately 100 individual juvenile chum salmon from each seine haul were checked for fin clips. We assumed negligible regeneration of clipped fins during the 3 mo sampling period. A subsample of 5–50 juvenile chum salmon was preserved in 10% formalin or 95% ethanol for length measurements and stomach content analysis or age determination, respectively. The remaining fish were released. Fork lengths of all preserved fish were measured to the nearest mm. These lengths were converted to fresh fish lengths or weights from the regressions of individual preseved lengths and weights on fresh lengths and weights (Wilson and Pearcy 1985a, b).

For data analysis, the 1984, 1985, and 1986 field seasons were divided into 21, 17, and 18 sampling periods, respectively, in which every beach seine station was usually sampled at least once. Stations were divided into the lower bay (stations 1–4, 12–14, and 22) and upper bay (stations 5–11, 15–21, and 23–26) (Fig. 1). Sand sediments predominate in the lower bay, whereas fine sands and silt, with high organic carbon, are common in the extensive tidal flats of the upper bay (Kreag 1979). Ninety-five percent confidence intervals of the median number of fish caught per set were calculated by the method presented in Snedecor and Cochran (1980). Mean lengths of fish from different regions of the bay were compared using a t-test for unequal variances (Sokal and Rohlf 1981). Growth rates among years were estimated from regressions of the size of recaptured marked fish and compared, using analysis of covariance (Snedecor and Cochran 1980). Growth in weight was calculated from length-weight regressions.

The total numbers of juvenile chum salmon remaining in the bay were estimated by a modified Peterson model (Healey 1980), where on day t,

$$N_t = \frac{CM}{R} \quad (1)$$

where N_t = total population,
C = total catch,
M = estimated number of marked fish present in the bay, and
R = number of marked fish recaptured.

The estimated number of marked fish present, M, was calculated assuming a constant loss rate of marked fish with time:

$$M = M_0\, e^{-kt}$$

where M_0 = total number of marked fish released,
k = instantaneous rate of disappearance of marked fish, and
t = days since release.

The actual number of marked fish recaptured and the estimated number of marked fish from each release group were pooled for each year and used in a modified Peterson model to estimate population numbers (N_t). The instantaneous rate of disappearance of marked fish was estimated for each marked group by the slope of the regression of time on catch per effort. This instan-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service. NOAA.

[2]Research Nets, Inc., Bothell, WA.

taneous loss rate, k, also provided an estimate of the residence time for each marked group in the estuary. Solving Equation (2) for t when $M/M_0 = ½$ gave the residency half-life in days, the time in which the number of fish had declined by 50%.

The estimated number of fish in the estuary (N_t) was multiplied by the average weight of marked fish to estimate the biomass of juvenile chum salmon present during each sampling period. These biomass estimates were multiplied by the number of days between sampling periods, summed over the entire period that juvenile chum salmon were present, and multiplied by an average instantaneous growth rate in weight of the marked groups to estimate net production for each year.

RESULTS

Emigration from Fresh water

We estimated an outmigration of 11,900, 23,300, and 15,300 chum salmon fry from Whiskey Creek in 1984, 1985, and 1986, respectively. The early portion of the run was not sampled in 1984. These estimates of naturally reared chum salmon fry equalled 1.4%, 6.2%, and 2.3% of the total chum salmon releases from the Whiskey Creek Hatchery in these years (Table 1). The abundances and temporal changes in catches of chum salmon were similar in Jackson and Whiskey Creeks in 1986 (Fig. 2). Since nearly all wild chum salmon spawned in Whiskey Creek or Jackson Creek, we assumed that the production of fry from naturally spawning chum salmon in the tributaries of Netarts Bay was about twice that of Whiskey Creek. The mean length of chum salmon fry caught was 40 mm in each of the three years in Whiskey Creek, and 41.0 mm in 1986 in Jackson Creek. Large fry (>45 mm), which were indicative of rearing in freshwater (Mason 1974), were not caught.

Nearly all wild chum salmon fry outmigrated into Netarts Bay by the end of April in all years (Fig. 2). Peak numbers of fry were caught in Whiskey Creek on 25 March 1984, 25 March 1985, 11 April 1985, and 8 April 1986. Numbers of emigrating fish were poorly associated with any measured physical variable. Peak catches of chum fry were not correlated with stream temperatures (Fig. 2), although the second outmigration pulse in 1985 followed an abrupt increase in water temperature. Increased outmigration activity of fry was not associated with phases of the lunar cycle as has been reported for other salmonid fry (Reimers 1973; Mason 1975). Stream flow estimated from stream heights appeared positively correlated with peak numbers of emigrating fry in 1984 when large numbers of fish were sampled during or immediately after three of four periods of high flow. The first peak of outmigration in 1985 also occurred during high stream flow; however, subsequent peaks in 1985 and 1986 occurred during periods of declining flow.

Distribution-Abundance in Netarts Bay

Chum salmon were present in Netarts Bay for about 2½ months, from mid-March until early June during each year (Fig. 3). The seasonal abundances of juvenile chum salmon in Netarts Bay were correlated with the emigration of wild fish from streams and with releases of fish from the Whiskey Creek Hatchery facility. Although small peaks in beach seine catches during late March 1984 and in early April 1986 coincided with the peak of outmigration of wild fish from Whiskey Creek, most of the naturally reared fry migrated into the bay before the major peaks in beach seine catches (Figs. 2, 3). The largest peaks in beach seine catches occurred within a few days after releases from the Whiskey Creek Hatchery in all years.

Catches of juvenile chum salmon were greater in the upper than the lower bay during March and April in all years. Conversely, catches were generally greater in the lower than the upper bay during May and June (Fig. 4). These trends indicate that juvenile chum salmon preferentially inhabited the upper bay early in the spring and then moved into the lower bay in late spring. Movement into the lower bay late in spring was correlated with the high water temperatures that occurred in the upper bay during May of each year.

Juvenile chum salmon appeared to avoid temperatures exceeding 14°C. Although they occurred at most temperatures observed in the upper bay during March and April, they usually inhabited waters of minimum temperatures during May and June, when average water temperatures exceeded 14°C (Fig. 5, left panel). The occurrence of juvenile chum salmon predominantly in the upper bay in early spring coincided with average upper bay temperatures of <15°C. Movements to the lower bay (Fig. 4) coincided with upper bay temperatures exceeding 16°C (Fig. 5, right panel). The percentages of chum

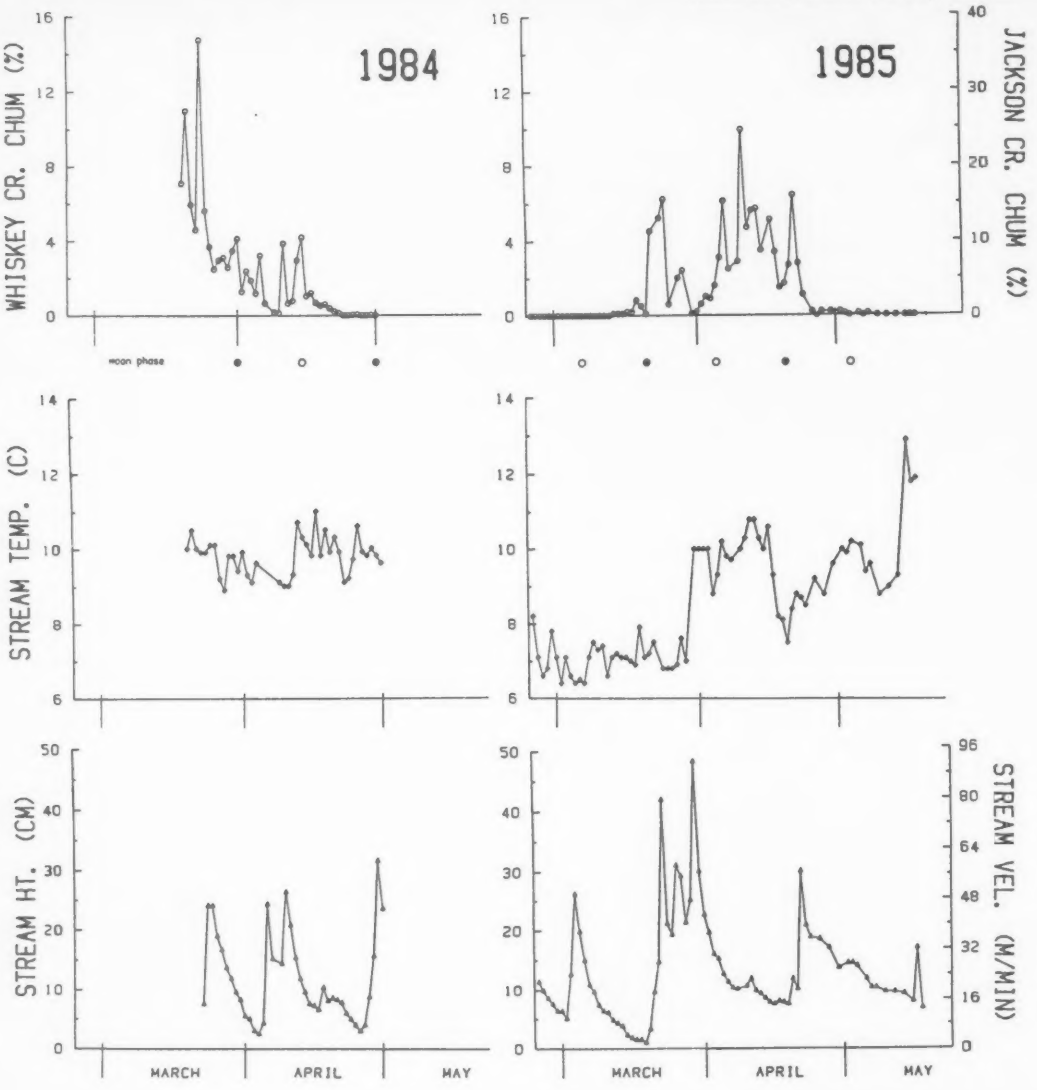

FIGURE 2.—Outmigration of juvenile chum salmon, stream temperatures, and stream height-velocity of Whiskey Creek (1984, 1985, 1986) and Jackson Creek (1986). Solid triangles indicate dates of hatchery releases.

salmon in the upper bay increased only once in all three years when temperatures exceeded 16°C (Fig. 5, 1985).

Schools of chum salmon were sometimes observed in shallow water and variability in the catches of juvenile chum salmon per set was high. The median number of chum caught per set during a sampling date, all stations combined, ranged from 0 to 280. A total of 90 pairs of beach seine sets were made during the three years. The mean (± standard deviation) of the quotient of the largest to smallest numbers of chum caught in the 47 pairs of two sets (each set containing fish) was 5.9 ± 8.8. This indicates that juvenile chum salmon were aggregated in Netarts Bay.

Median catches of juvenile chum salmon during high tide generally exceeded catches at low tide in March and April, and catches at low tide were greater than high tide during May and

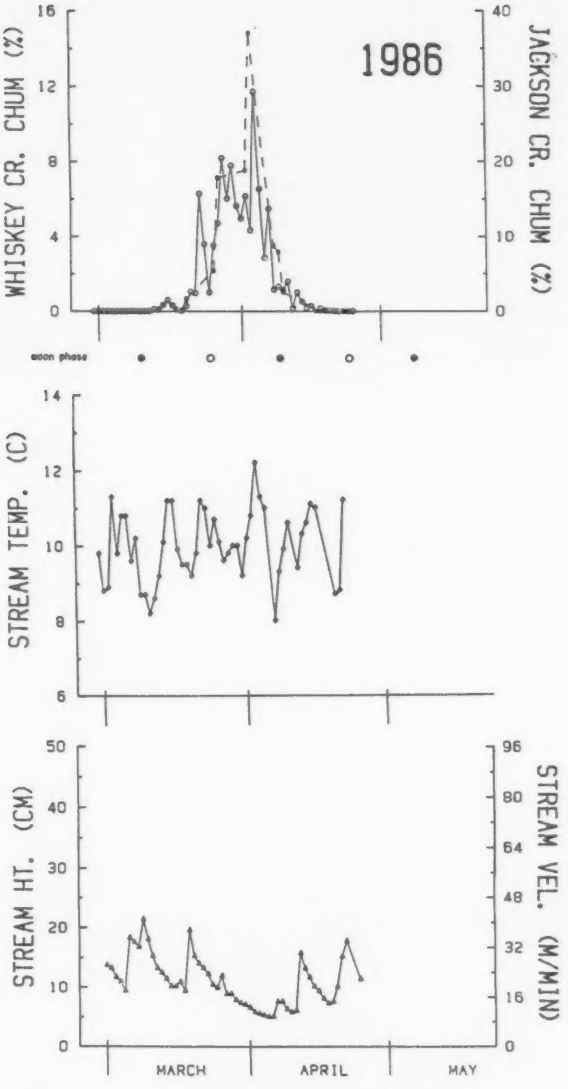

FIGURE 2.—*Continued.*

June of 1984 and 1985 (but not 1986) (Fig. 6). The large catches of juvenile chum salmon along the margins of the bay at high tide, often over 500 m from the low-tide channels in the upper bay, show that they make extensive tidal excursions over the tidal flats during daylight in early spring and actively aggregate along the fringes of the estuary in shallow water.

Juvenile chum were not concentrated in the main channel of lower Netarts Bay between 25 March and 20 June 1985 when tow net hauls were made. Only 38 juvenile chum salmon were caught in the 31 tows (about one fish per 2,000 m^2). Catches in night tows on 22 May were not different from day tows on 21 May (Mann-Whitney U test, $P > 0.1$). Also, the average lengths of chum salmon fish caught in day and night tow net collections and in beach seine collections on 22 May were not significantly different (t-test, $P > 0.1$).

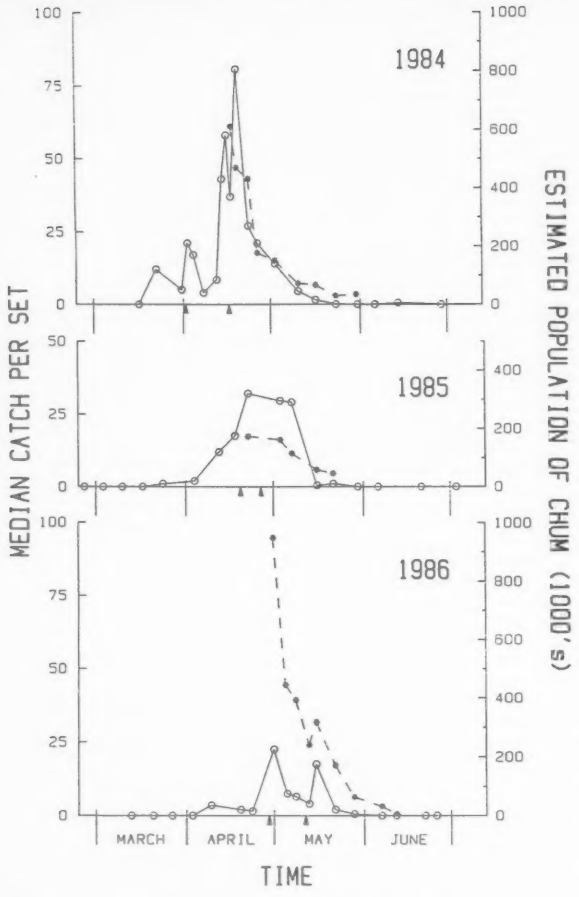

FIGURE 3.—Median catch per beach seine haul of juvenile chum salmon, from all stations combined (solid line) and population estimates based on recaptures of marked fish (dashed line).

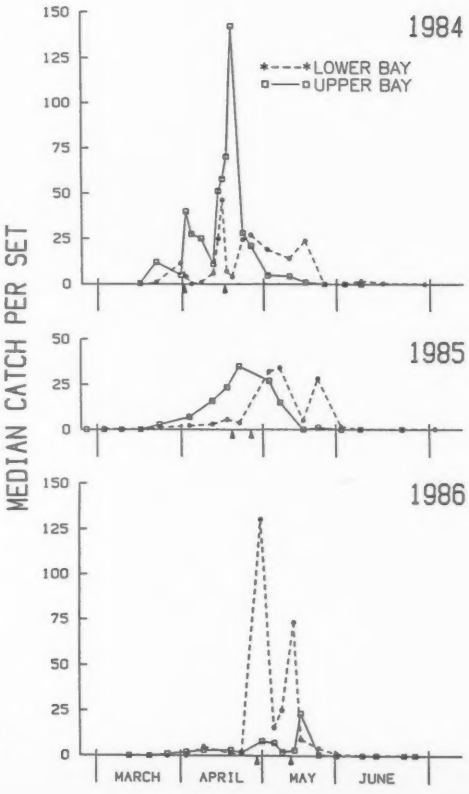

FIGURE 4.—Median catch per seine haul of juvenile chum salmon in the upper (solid line) and lower (dashed line) estuary, and release dates (black triangles).

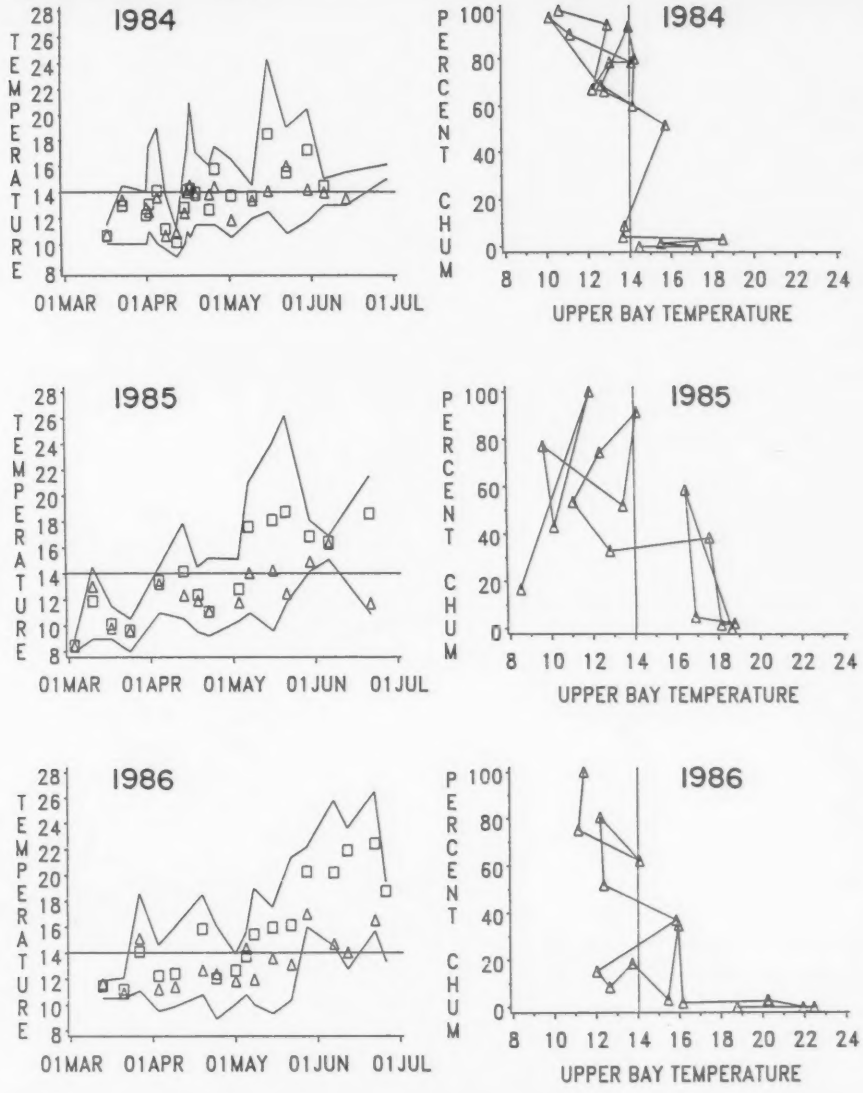

FIGURE 5.—(Left) average temperatures occupied by chum salmon (triangles), average upper bay temperatures (squares) and maximum and minimum temperatures temperatures per collection period (solid lines), and (Right) the percent of juvenile chum salmon collected in upper bay stations vs. average upper bay temperatures (lines connect sequential sampling periods) for 1984, 1985, and 1986. Reference lines indicate 14°C.

Residence Times – Loss Rates

Population estimates based on the total catch showed that the number of marks present, and numbers of marked fish recaptured (Equation (1)), rapidly declined during 1984 and 1986 (Fig. 3 dashed lines; Table 2). The trends shown by mark and recapture estimates and by median seine haul catches were similar in 1984 (Fig. 3). Population estimates on 17 and 18 April 1984 and 3 and 4 May 1985 (1–2 days and 7–8 days after release of all marked fish) were 30% and 57% smaller than the actual numbers of fish released, suggesting rapid decline in numbers soon after release. In 1986, however, the initial population estimate was 55% larger than the number of fish released a week earlier. Marked fish released in April 1986 probably experienced higher mortal-

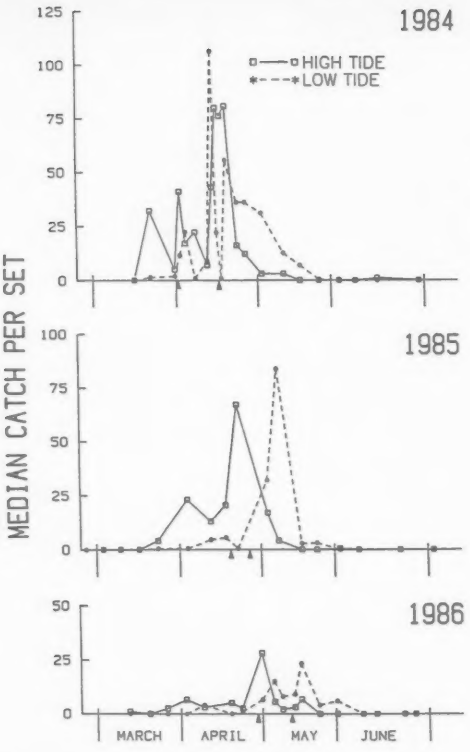

FIGURE 6.—Median catches per seine haul of chum salmon at high tide (solid line) and low tide stations (dashed line), 1984–86. Solid triangles indicate dates of hatchery releases.

ity after release than unmarked fish as a result of the added stress of marking and the debilitating bacterial disease that afflicted this release group. As a result of higher mortality of marked fish, R was low and M was probably overestimated, leading to overestimation of the population (N_t, Equation (1)).

Higher loss rates were found for small than for large fish hatchery chum salmon in Netarts Bay from the decline in the natural logarithm of catch per effort of fin-clipped fish (Table 3). In 1986, the residence half-life (the time for the catch rates to decrease by one-half (Myers and Horton 1982)) was 7.4 days for fish released at 1.0 g, 4.9 days for fish released at 2.2 g and <2 days for fish released at 6.5 g. None of the largest fish was captured 2 days after release or during subsequent sampling. Presumably these large fish emigrated rapidly from the estuary. An anomaly in the trend for loss rates to be positively correlated with size of juvenile chum salmon released arose for the 1.9 g right ventral (RV) clipped fish in 1984. Their residency half-life was 16 days, about the same as for 0.75 g fish released on the same day, and three times that of 1.9 g fish released in 1985 (Table 3). The significantly higher ($P < 0.01$, analysis of covariance) residency half-lives of fish released in 1984 than in other years may have arisen because these fish were released earlier in the spring. In other years, early release groups also had longer half-lives than later groups, but the slopes of the catch vs. time were not significantly different ($P > 0.05$).

Juvenile chum salmon actively maintained themselves in the bay. Residency half-lives of marked chum were 10–30 times longer than predicted from random loss with tidal flushing. Assuming that the mean intertidal volume of Netarts Bay is 75% of the total volume at MHW (Glanzman et al. 1971; Kreag 1979) and does not reenter the bay on subsequent tidal cycles, the half-life of water in Netarts Bay is <0.5 day.

Growth

Instantaneous growth rates in weight of fin-clipped chum salmon averaged 1.6–2.3% body weight per day (Table 3). No differences (analysis of covariance, $P > 0.05$) were found in growth in weight among these groups released within or among years. However, linear growth rates estimated from changes in fork length over time indicate that fish released at a smaller size grew more rapidly in 1984 (0.48 mm/d for 46 mm fish vs. 0.41 mm/d for 52 mm fish) and in 1986 (0.53 mm/d for 48 mm fish vs. 0.33 mm/d for 62 mm fish). Growth rates were similar for both 56 mm vs. 59 mm fish in 1985. Slopes derived from linear regression of mean individual lengths of all fish during a sampling period vs. elapsed time in days did not differ significantly ($P > 0.05$) from the rate of increase of lengths of marked fish in 1984, 1985, or 1986. These slopes were also similar among years. Increases in mean length probably reflected growth. None of the regressions of FL vs. time showed trends for decreasing size late in the spring that would be due to emigration of large individuals from the bay.

Biomass-Production

The biomass of juvenile chum salmon in Netarts Bay, estimated from population numbers (N_t) and average weight of the marked groups of fish during the week after release of

TABLE 2.—Estimates of the mean weight and length, of the population numbers based on marked fish, of the population biomass, and of the cumulative production of juvenile chum salmon in Netarts Bay, 1984–86.

	Average (g)	Average (mm)	Estimate number × 1000 (N_t)	biomass (kg)
1984				
17–18 April	1.6	56	610.5	977
19–20 April	1.6	56	468.0	772
23–24 April	1.9	59	429.6	816
26–27 April	1.8	58	176.6	323
2–3 May	1.9	58	150.3	280
10–11 May	2.1	62	71.1	151
16–17 May	2.1	62	65.9	141
23–24 May	2.9	62	28.6	84
30–31 May	3.2	71	34.2	109
Cumulative biomass (45 d)(kg)		13,591		
Instantaneous growth rate		0.02075		
Total production (kg)		282		
22–23 April	1.5	54	173.3	253
3–4 May	1.8	58	161.1	284
7–8 May	1.8	58	114.7	207
15–17 May	2.2	63	58.3	130
21–22 May	1.9	60	46.0	89
Cumulative biomass (19 d)(kg)		6,169		
Instantaneous growth rate		0.01675		
Total production (kg)		103		
1986				
1 May	0.8	45	947.4	805
5 May	1.0	47	444.5	449
8–9 May	1.1	49	392.6	440
13 May	1.4	53	240.0	331
15–16 May	1.4	53	317.3	444
21–3 May	1.7	57	171.1	294
28–29 May	1.9	60	63.4	122
7 June	2.6	65	30.6	78
12 June	2.6	66	5.3	14
Cumulative biomass (45 d)(kg)		11,154		
Instantaneous growth rate		0.0211		
Total production (kg)		235		

TABLE 3.—Data on the releases into Whiskey Creek, and the residency half-lives and growth rates of marked juvenile chum salmon in Netarts Bay, 1984–86.

Release data	Length at release (mm)	Weight at release (g)	Mark	Residency half-life (d)	Growth rate (% wt/d)
1984					
16 April	46	0.75	LV	14.94	2.27
16 April	58	1.9	RV	15.89	1.88
1985					
19 April	56	1.8	RV	5.54	1.61
26 April	59	1.9	LV	4.95	1.74
1986					
28–29 April	48	0.97	RV	7.38	2.26
11 May	62	2.2	RV + A	4.92	1.96
11 May	92	6.5	LV + A	<2.0	

both groups of marked hatchery fish, were estimated about 800–980 kg in 1984, 250–280 kg in 1985, and 450–800 kg in 1986 (Table 2). Increases in the biomass, indicative of accumulation of biomass from growth exceeding loss of biomass from migration or mortality, were not apparent in any year.

Total production or net growth of juvenile chum salmon (a product of the cumulative biomass over all days after the release of marked fish times the instantaneous growth rate of marked fish) measured 282 kg, 103 kg, and 235 kg in 1984, 1985, and 1986, respectively (Table 2). Total production is underestimated because production before the release of marked fish is not included. These production estimates are only 32%, 38%, and 37% of the estimated average biomass of the first two collection periods after releases in 1984, 1985, and 1986, respectively.

DISCUSSION

Netarts Bay is an important nursery area for juvenile chum salmon. Despite the small size and high flushing rate of Netarts Bay, juvenile chum salmon were captured during about a 2 mo duration in all three years. This is about the same duration as reported for wild juvenile chum salmon in Yaquina Bay, Oregon (Myers and Horton 1982), but is less than the three or more months reported for Tillamook Bay, Oregon (Henry 1953; Forsberg et al. 1977), Grays Harbor, Washington (Herrmann 1970), the Skagit River salt marsh, Washington (Congelton et al. 1982), and the Nanaimo Estuary, British Columbia (Healey 1979, 1982a). Juvenile chum salmon were reported in Hood Canal from January through July by Bax (1982). The mean residence times (see Healey 1979 for equation) of marked groups of hatchery-reared juvenile chum salmon (0.75–2.2 g at release) ranged from 5 to 23 days in Netarts Bay. These residence times are about the same as those found by Healey (1979) in the Nanaimo Estuary, but were more than the residence time of about 2 days in a small tidal channel reported by Congelton et al. (1982). Clearly, juvenile chum actively maintain themselves in many estuaries during early development.

Catches of juvenile chum salmon in the bay declined rapidly over time. The proportions lost from emigration and mortality are difficult to separate. Healey (1982a) concluded that some fish immediately emigrated from the Nanaimo and Nitinat Estuaries. Bax (1982) reported initial dispersal of marked hatchery fish, and net movements of 3–14 km/d for juvenile chum salmon in the elongated fjord of Hood Canal that would rapidly remove chum salmon from a small estuary. Lannan (1983) noted fish and bird predation on juvenile chum salmon in Netarts Bay. Most of the fish predation was caused by cutthroat trout, *Oncorhynchus clarki*, during downstream migration of chum fry and by Pacific staghorn sculpin, *Leptocottus armatus*, as fry entered the bay (J. Lannan, pers. comm.[3]). We examined 57 large (>100–215 mm FL) staghorn sculpin, 34 cutthroat trout (95–365 mm FL), and 28 coho salmon (95–156 mm FL) caught in our beach seine collections in Netarts Bay and found three juvenile chum salmon in staghorn sculpin stomachs and one in a coho salmon stomach. Gulls, mergansers, cormorants, and herons were common in the bay, but we have no data on their food habits. Harbor seals, *Phoca vitulina*, were also common in Netarts Bay in late spring; their scats were analyzed, but otoliths of juvenile salmon were not identified (Brown and Mate 1983), perhaps because the smallest sieve they used had a mesh size of 0.5 mm, a mesh that would retain otoliths of only large juvenile chum.

The distribution of juvenile chum salmon in Netarts Bay, with higher catches generally in the upper than lower bay early in the spring, and the reverse later in the spring is similar to that found by Healey (1979, 1982a) in the Nanaimo Estuary, by Myers and Horton (1982) in Yaquina Bay, and by Forsberg et al. (1977) in Tillamook Bay; but in the Nitinat Estuary no evidence of seaward progression was found (Healey 1982a). In Netarts Bay, juvenile chum salmon moved extensively over the tidal flats, aggregating in shallow water during periods of both high and low tide (cf. Mason 1974; Forsberg et al. 1977; Healey 1979, 1982a). In late spring, fish curtailed their movements into shallow warm waters of the upper bay at high tide and were concentrated instead in the lower estuary.

Based on limited pelagic sampling, we found no evidence for movement of fish into the deep channel areas of the lower bay later in the season. Juvenile chum salmon larger than 45–55 mm were caught in large numbers at some shallow seine stations in the lower bay in May and June. Some individuals were as large as 89

[3]J. Lannan, Oregon State University, Hatfield Marine Science Center, Newport, OR 97365, pers. commun. 22 December 1988.

mm and over 4 g wet weight. Fish averaged over 60 mm and 2 g by the end of May in all years (Table 2). Many juvenile chum salmon apparently stayed in shallow water in Netarts Bay beyond the size of 45–55 mm, the length at which they are thought to migrate from shallow estuarine waters into open neritic waters of other estuaries (Kaczyinski et al. 1973; Healey 1980a, 1982b; Simenstad and Salo 1980; Myers and Horton 1982). Large chum salmon apparently did not aggregate in the deep channels of Netarts Bay but emigrated directly out of the bay into open coastal waters.

The average size of juvenile chum salmon increased during their residence in Netarts Bay, as well as in Tillamook Bay (Forsberg et al. 1977), Yaquina Bay (Myers and Horton 1982), and Grays Harbor (Herrmann 1970). This increase suggests growth. Since large chum salmon are thought to emigrate more rapidly than small chum (Healey 1982a) and recruitment of downstream migrants may be prolonged, these estimates based on size-frequency distributions probably underestimate growth rates. The growth rates for marked chum salmon in Netarts Bay, 0.4–0.6 mm/d and 1.6–2.3% body weight (BW)/d, may also be underestimates if rapidly growing fish exit the bay sooner than slow growing fish. Growth rates of juvenile chum salmon in Netarts Bay are considerably less than the 1 mm/d and 6% BW/d estimated from marked juvenile chum in the Nanaimo Estuary (Healey 1979, 1982a) and the 8.6% BW/d for marked chum in Hood Canal (Bax and Whitmus 1981), but they are more similar to the 0.8 mm/d and about 4.2% BW/d for unmarked juvenile chum salmon in the Fraser River and Gulf Islands (Phillips and Barraclough 1978; Healey 1982b), the 2.7% BW/d for unmarked chum in Nitinat Lake, and the 0.4 mm/d found for unmarked chum in Steamer Bay, southeastern Alaska (Murphy et al. 1988). They are also similar to the growth rates of juvenile chum reared in saltwater aquaria at daily rations of 6–10% BW/d (Volk et al. 1984).

The cumulative biomass of juvenile chum salmon in Netarts Bay (13.6, 6.2, and 11.2 $\times$ 10^3 kg) was generally lower than the 14–66 $\times$ 10^3 kg estimated for naturally reared chum salmon in the similarly sized Nanaimo Estuary by Healey (1979). Total production of juvenile chum in the Nanaimo Estuary during the two years studied was 1,100–2,400 kg (or 0.2–0.4 g/m^2 of intertidal area), over an order of magnitude higher than that estimated in Netarts Bay (0.01–0.03 g/m^2 of intertidal area). This suggests that the carrying capacity of Netarts Bay for juvenile chum is limited. However, we found no evidence for density-dependent growth. Growth rates and residence times were about the same among years with several-fold differences in numbers of fry released and estimated biomass of juvenile chum salmon in the estuary (Tables 1, 2, 3). Production may be limited by the short residence times of large hatchery fish released late in the spring as well as by environmental factors other than direct competition for food.

Elevated water temperatures may affect growth of juvenile chum salmon, especially since Netarts Bay is at the southern extremity of the spawning range of this species in the northeastern Pacific Ocean. Kepshire (1971) reported an optimum temperature of 13°C for growth of juvenile chum salmon, and at 15°C, a temperature often recorded in Netarts Bay, food consumption was higher than at lower temperatures, but food conversion efficiency and growth were low. Irie (1984) found that ocean temperatures where juvenile chum salmon were found along the coast of Hokkaido were below 14°C. Juvenile chum salmon in Netarts Bay may also be excluded from the best foraging habitat by high temperatures. Densities of crustacean prey were highest in the intertidal areas of the upper bay (Chapman unpubl. data) where highest temperatures occurred. Costs of metabolism, food conversion, prey capture, and swimming may limit allocation of energy to growth when temperatures are above optimal (Brett 1979; Wissmar and Simenstad 1988).

Growth efficiencies may also be influenced by the quality and quantity of available prey. Small harpacticoid copepods (viz., *Harpacticus uniremis*) have been found to predominate the diet of juvenile chum salmon in estuaries (Healey 1979; Sibert 1979; Simenstad and Salo 1980; Simenstad and Wissmar 1984) where growth rates are high, whereas large amphipods predominated the diet in Netarts Bay (Chapman, unpubl. data), and mollusk larvae, hyperiid amphipods, and larvaceans were important prey for juvenile chum salmon in Steamer Bay, AK (Murphy et al. 1988) where growth was slower. Large prey, such as amphipods, may require more energy to capture because of highly developed escape responses (Volk et al. 1984), may be digested less efficiently because of their thick chitinous exoskeletons (Pandian 1967; Brett and Groves 1979), and may have lower per unit weight caloric value (Cummins and Wuycheck

1971) than smaller prey, such as harpacticoid copepods. Volk et al. (1984) reported that food conversion efficiency was much higher for juvenile chum salmon fed harpacticoid copepods than larger amphipods. All these factors could affect growth. Furthermore, pelagic calanoid copepods, hyperiid amphipods, and larvaceans, known to be important prey for large (>45 mm) juvenile chum salmon as they move to open neritic waters (Simenstad and Salo 1980), were not abundant in Netarts Bay, perhaps further constraining growth and production in this small estuary.

A possible strategy to circumvent the need for estuarine rearing where habitat quality limits production is to release juvenile chum salmon at a large size. Healey (1980a, 1982a) observed that seaward movement of juvenile chum salmon is size-dependent, with large fish moving offshore first. Juvenile chum salmon entering estuaries late in the spring also emigrate after a short time (Sibert et al. 1977; Ioka 1978). In Japan, juvenile chum salmon reared in salt water (Kobayashi 1980) migrate to the open sea within a week after release and chum salmon reared to a large size (8 g) return to hatcheries at a high rate (Ioka unpubl. data).

Our experimental releases of different sizes of fry indicate that large juvenile chum salmon do not utilize Netarts Bay as a nursery area. The large (6.5 g) chum we released in 1986 apparently migrated immediately to the ocean. When these fish returned to Whiskey Creek as adults in 1988 (presumably at age 3, based on the age structure of previous runs (Lannan 1983; J. Fisher unpubl. data)), the ratio of fish with missing left: right ventral fins was 2:1 (W. McNeil, pers. commun.[4]). This ratio was 0.6:1 in the juvenile chum salmon released in 1986 (Table 1). This suggests that these large (6.5 g) juvenile chum salmon that were not dependent on the estuary survived at rates that were 3–4 times higher than the smaller (1.0–2.2 g) fish released that year. More experiments are needed to confirm these results. Rearing chum salmon fry to a large size may be a useful method to enhance hatchery runs into estuaries, especially if size-selective predation is intensified by retarded growth owing to high temperatures or low availability of prey. Furthermore, large hatchery fish released late in the spring may have minimal adverse impacts on wild stocks.

[4]W. McNeil, Oregon State University, Hatfield Marine Science Center, Newport, OR 97365, pers. commun., 5 December 1988.

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Larval Fish Diets in Shallow Coastal Waters off San Onofre, California

William Watson and Raymond L. Davis, Jr.

ABSTRACT: Stomach contents were analyzed from the larvae of six common coastal fish taxa (*Atherinopsis californiensis, Leuresthes tenuis, Paralabrax* spp., *Genyonemus lineatus, Seriphus politus,* and *Paralichthys californicus*) collected near San Onofre, California. Samples were collected at night at approximately monthly intervals between September 1978 and September 1979 during a study of ichthyoplankton distributions in these shallow coastal waters.

***Paralabrax* spp. and *Paralichthys californicus* larvae apparently did not feed at night, but high feeding incidences for the atherinids and especially the sciaenids suggested that these larvae did feed during early evening hours. Important components of the diets of all six taxa included the tintinnid genus *Stenosomella*, mollusc veligers, and especially the copepod *Euterpina acutifrons*.**

The vertical distributions of the fish larvae differed from the reported distributions of some of their principal prey taxa, suggesting that factors in addition to, or other than, specific feeding habits are important determinants in the nearshore distributions of fish larvae. The avoidance of seaward dispersal away from the relatively productive and stable nearshore zone may be an important factor influencing larval distribution.

Most studies on the feeding habits of fish larvae in the Southern California Bight have focused on species whose larvae occur primarily beyond the continental shelf, or are broadly distributed across the shelf and beyond (Arthur 1956, 1976; Hunter and Kimbrell 1980; Lasker 1975; Sumida and Moser 1980, 1984; Theilacker 1986). Larval fish feeding in the shallow coastal zone (depth ≤75 m) has, until recently, received relatively little attention. Lasker (1975, 1981) examined the requisite conditions for the successful first feeding of larval northern anchovy and suggested that the shallow nearshore zone may provide a better larval feeding environment than offshore waters, largely because of the more stable nature of the nearshore zone.

It has become increasingly apparent in recent years that this shallow nearshore zone is a unique area supporting distinctive, stable assemblages of fish larvae and zooplankters (Brewer et al. 1981, 1984; Gruber et al. 1982; Barnett et al. 1984; Brewer and Kleppel 1986; Petersen et al. 1986; Barnett and Jahn 1987; Walker et al. 1987). Feeding studies are beginning to be reported for some of the fish larvae that are largely restricted to this zone (Brewer and Kleppel 1986; Jahn et al. 1988).

The purpose of this report is to document the food habits of the larvae of six fish taxa in the shallow coastal waters off southern California. These six taxa include larvae occupying all levels of the water column: larval jacksmelt, *Atherinopsis californiensis*, and grunion, *Leuresthes tenuis*, are largely restricted to the neuston and upper water column; California halibut, *Paralichthys californicus*, and kelp and sand bass, *Paralabrax* spp., larvae occur throughout the water column but tend to be most abundant in midwater; and larval queenfish, *Seriphus politus*, and white croaker, *Genyonemus lineatus*, occur principally in the lower water column and epibenthos (Schlotterbeck and Connally 1982; Barnett et al. 1984; Jahn and Lavenberg 1986). All six taxa occur principally near shore throughout life (Frey 1971; Miller and Lea 1972; Barnett et al. 1984; Lavenberg et al. 1986;).

METHODS

Plankton samples were collected between 25 July 1978 and 23 September 1979 near San Onofre, CA (lat. 33°20′N, long. 117°30′W). The plankton sampling methodology and rationale are detailed by Barnett et al. (1984) and Walker et al. (1987) and are only briefly summarized here.

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Two sample sets, both of which provided complete water column coverage, were utilized in this study. A small sample set, used to make a rough approximation of feeding chronology, consisted of plankton samples collected twice during the day and twice at night within a 24 h period, on two occasions (25 July and 21 September 1978). These samples were collected along the 8 m isobath 1 km south of the San Onofre Nuclear Generating Station (SONGS) (July) and along the 13 m isobath just north of SONGS (September). A larger sample set, used to examine larval diets, consisted of plankton samples collected at night at approximately monthly intervals between 6 September 1978 and 23 September 1979, along a randomly selected isobath within each of five offshore blocks. These blocks were defined by depth contours: (A) 6–9 m, (B) 9–12 m, (C) 12–22 m, (D) 22–45 m, and (E) 45–75 m. The blocks were arrayed between 0.5 and 7.2 km from shore, approximately 1 km south of SONGS.

SONGS Unit 1, a 500 megawatt power plant, operated throughout the study period. Unit 1 has been shown to have had only very localized effects (Marine Review Committee 1979[1]) and it is unlikely to have influenced the results of this study.

Three different types of gear were used to collect both sample sets: a Brown Manta net (Brown and Cheng 1981), to sample the neuston (top 16 cm); a Brown-McGowan opening-closing bongo net, to sample the midwater column; and an Auriga net[2], to sample the epibenthos (within approximately 67 cm of the bottom). All three types of nets were constructed of 0.333 mm mesh Nitex[3], fitted with flowmeters, and towed at ca. 1 m/s to sample a target volume of 400 m^3. All samples were fixed in 10% seawater-formalin.

In the laboratory, the plankton samples were subsampled with a folsom plankton splitter and the fish larvae were sorted from the subsamples at 6–10× magnification under dissecting microscopes. Larvae utilized in the feeding studies were randomly selected from among those sorted from a subsample; a maximum of 100 specimens was selected from any subsample. These larvae were measured to the nearest 0.1 mm notochord or standard length, separated by developmental stage (preflexion = Pr; notochord flexion plus postflexion = FP), placed in a glycerin-water solution, and dissected with fine insect pins. The gut contents of each specimen were identified to the lowest possible taxon using a dissecting (50×) or compound (100–450×) microscope, as appropriate, and enumerated. The number of specimens dissected is listed by species, survey, and sample in Table 1.

Feeding incidence (%FI = percentage of larvae examined that contained at least one food item) was calculated with 95% confidence limits for each larval stage of each taxon. The 95% confidence limits were approximated as $\pm 1.96 (pq/n)^{1/2} + 1/2n$, where p = the proportion containing at least one food item, $q = 1 - p$, and n = the sample size. Percent frequency of occurrence (%FO) and percent of the total number (%N) of prey ingested by each larval fish stage were calculated for each prey type.

RESULTS

Feeding Chronology

Feeding incidence was calculated for *Seriphus politus*, *Paralabrax* spp., and *Paralichthys californicus* which were collected in the day/night sample sets in order to examine feeding chronology (Table 2). Larval *Genyonemus lineatus* and *Atherinopsis californiensis* did not occur in these samples, and too few *Leuresthes tenuis* were available to warrant examination.

During the day, 82% of the *S. politus* larvae contained at least one food item, while at night, 72% contained food. Feeding incidence increased from the morning through the evening, reaching a maximum of 94% for the larvae collected between 2003 and 2101 PST. However, since the feeding incidences were all quite high, and the 95% confidence limits about %FI broadly overlapped for all three morning through evening sampling episodes, it seems likely that there were no real differences in feeding incidence over this period. After midnight, feeding incidence was reduced to 33%, and the 95% confidence limits did not overlap with either the morning or evening values, indicating that feeding incidence indeed was reduced after midnight (Table 2).

Paralabrax spp. feeding incidence was 68%

[1]Marine Review Committee. 1979. Interim report of the Marine Review Committee to the California Coastal Commission part 1: General summary of findings, predictions, and recommendations concerning the cooling system of the San Onofre Nuclear Generating Station. Mar. Rev. Comm. Doc. 79–02, p. 1–20. Marine Review Committee of the California Coastal Commission, 631 Howard Street, San Francisco, CA 94105.

[2]MBC Applied Environmental Sciences, 947 Newhall Street, Costa Mesa, CA 92627.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Number of fish larvae dissected on each survey date. Pr = preflexion stage larvae; FP = flexion and postflexion stage larvae.

Survey date	*Atherinopsis californiensis*		*Leuresthes tenuis*		*Paralichthys californicus*		*Paralabrax spp.*		*Genyonemus lineatus*		*Seriphus politus*	
	Pr	FP	Pr	FP	Pr	FP	Pr	FP	Pr	FP	Pr	FP
1978												
06 Sept.	0	0	0	24	2	3	30	9	0	0	107	86
02 Oct.	1	0	0	10	15	1	0	0	39	4	13	26
01 Nov.	0	0	0	0	49	1	1	3	17	5	3	2
26 Dec.	2	5	0	0	31	7	0	0	89	33	0	0
1979												
29 Jan.	0	0	0	0	10	0	0	0	138	94	0	0
26 Feb.	2	31	0	0	41	2	0	0	146	98	0	0
26 Mar.	20	21	0	0	0	0	0	0	161	180	23	0
25 Apr.	7	19	7	13	0	0	0	0	40	86	18	0
23 May	0	8	17	20	0	0	0	0	32	49	19	14
25 June	1	1	22	95	0	0	0	0	0	2	51	66
24 July	0	0	0	0	0	0	43	8	0	0	74	14
22 Aug.	0	0	0	9	3	0	13	2	0	0	58	32
20 Sept.	0	0	2	14	35	9	24	2	9	0	87	49
Total	33	85	48	185	186	23	111	24	671	551	453	289

TABLE 2.—Feeding chronology of larval *Paralabrax* spp., *Paralichthys californicus*, and *Seriphus politus*. Survey A samples were collected at the 8 m isobath on 25 July 1978; Survey B samples were collected at the 13 m isobath on 21 September 1978. The time of day when samples were collected is given as Pacific Standard Time. N_t = total number of specimens dissected; N_f = number of specimens containing food; % FI = percent feeding incidence (100 × N_f); 95% confidence limits (C.L.) are given for % FI.

Survey	Time (PST)	*Paralabrax* spp.			*Paralichthys californicus*			*Seriphus politus*		
		N_t	N_f	% FI ± C.L.	N_t	N_f	% FI ± C.L.	N_t	N_f	%FI ± C.L.
A	0547–0626							34	26	76.5 ± 15.7
B	0920–1024	20	11	55.0 ± 24.3	17	9	52.9 ± 26.7			
A	1103–1153							37	32	86.5 ± 12.4
B	1345–1420	14	12	85.7 ± 21.9	7	0	0.0 ± 7.1			
B	1900–1958	18	9	50.0 ± 25.9	26	7	26.9 ± 19.0			
A	2003–2101							70	66	94.3 ± 6.1
B	2354–0049	24	0	0.0 ± 2.1	20	3	15.0 ± 18.1			
A	0118–0150							39	13	33.3 ± 16.1

during the day and 12% at night. Feeding incidence was highest (86%) during midafternoon (1345–1420 PST), dropped to 50% within an hour after sunset, and was 0% by about midnight (Table 2). The 95% confidence limits about %FI were rather broad owing to the small sample sizes, and it is unclear whether there were any real differences in feeding incidence from morning through early evening. However, the large differences in %FI and nonoverlapping confidence limits between the morning through evening and midnight sampling episodes do indicate a real reduction in feeding incidence at night.

Paralichthys californicus larvae displayed a low feeding incidence: 38% during the day and 22% at night. More larvae contained food items during midmorning that at any other time; none contained food in the midafternoon samples (but only seven larvae were available for disssection in the afternoon samples). At night, feeding incidence decreased from 27% about an hour after sunset to 15% by about midnight (Table 2). However, owing to the small sample sizes and consequent broad confidence limits about %FI, it is unclear whether there were any real differences in feeding incidence over this period.

Composition of the Diet

Atherinopsis californiensis

Larval jacksmelt were collected almost exclusively in the neuston in the two sampling blocks (A and B) between the 6 and 12 m isobaths, from October 1978 to June 1979. In total, 118 specimens were dissected (Table 1); 47% of these contained food. The overall feeding inci-

TABLE 3.—Feeding incidence of fish larvae by block, depth stratum, and larval developmental stage. Blocks correspond and E = epibenthos. N_t = total number of larvae dissected; N_f = number of larvae containing food;

Block	Stratum	Number of larvae	*Atherinopsis californiensis*		*Leuresthes tenuis*		*Paralichthys californicus*	
			Preflexion	Flexion-postflexion	Preflexion	Flexion-postflexion	Preflexion	Flexion-postflexion
A	N	N_t	17	60	11	91	3	4
		N_f	10	31	3	48	2	0
		%FI	58.8 ± 26.3	51.7 ± 13.5	27.3 ± 18.0	52.7 ± 10.8	66.7 ± 70.0	0.0 ± 12.5
	M	N_t	2	1	0	2	5	3
		N_f	2	1	0	1	4	0
		%FI	100.0 ± 25.0	100.0 ± 50.0	—	50.0 ± 94.3	80.0 ± 45.1	0.0 ± 16.7
	E	N_t	0	0	0	0	2	1
		N_f	0	0	0	0	1	0
		%FI	—	—	—	—	50.0 ± 94.3	0.0 ± 50.0
B	N	N_t	11	25	13	31	8	1
		N_f	5	6	10	13	4	0
		%FI	45.5 ± 34.0	24.0 ± 18.7	76.9 ± 26.8	41.9 ± 19.0	50.0 ± 40.9	0.0 ± 50.0
	M	N_t	0	0	0	0	13	0
		N_f	0	0	0	0	2	0
		%FI	—	—	—	—	15.4 ± 23.5	—
	E	N_t	0	0	0	0	2	2
		N_f	0	0	0	0	1	0
		%FI	—	—	—	—	50.0 ± 94.3	0.0 ± 25.0
C	N	N_t	0	2	7	21	10	1
		N_f	0	0	6	3	1	0
		%FI	—	0.0 ± 25.0	85.7 ± 33.1	14.3 ± 17.4	10.0 ± 23.6	0.0 ± 50.0
	M	N_t	0	0	0	0	31	6
		N_f	0	0	0	0	12	2
		%FI	—	—	—	—	38.7 ± 18.8	33.3 ± 46.1
	E	N_t	0	0	0	0	15	0
		N_f	0	0	0	0	5	0
		%FI	—	—	—	—	33.3 ± 27.2	—
D	N	N_t	0	0	8	12	14	0
		N_f	0	0	0	1	4	0
		%FI	—	—	0.0 ± 6.3	8.3 ± 19.8	28.6 ± 27.2	—
	M	N_t	0	0	0	0	47	2
		N_f	0	0	0	0	11	0
		%FI	—	—	—	—	23.4 ± 13.2	0.0 ± 25.0
	E	N_t	0	0	0	0	9	0
		N_f	0	0	0	0	5	0
		%FI	—	—	—	—	55.6 ± 38.0	—
E	N	N_t	0	0	9	28	3	0
		N_f	0	0	0	0	0	0
		%FI	—	—	0.0 ± 5.6	0.0 ± 1.8	0.0 ± 16.7	—
	M	N_t	0	0	0	0	19	3
		N_f	0	0	0	0	3	2
		%FI	—	—	—	—	15.8 ± 19.0	66.7 ± 70.0
	E	N_t	0	0	0	0	4	0
		N_f	0	0	0	0	0	0
		%FI	—	—	—	—	0.0 ± 12.5	—

dence was a little higher for the Pr larvae (56.7 ± 19.4%) than for the older specimens (43.2 ± 10.9%). Both the younger and older larvae displayed a higher feeding incidence in the block nearest shore (Table 3). For the FP larvae summed over all strata, the 95% confidence limits about %FI barely overlapped between block A (52.5 ± 13.4%) and those farther seaward (22.2 ± 17.5%). For the Pr larvae, however, confidence limits broadly overlapped between block

to isobaths: A = 6–9 m; B = 9–12 m; C = 12–22 m; D = 22–45 m; E = 45–75 m. Strata are N = neuston; M = midwater; %FI = feeding incidence (100 × N_f/N_t). Ninety-five percent confidence limits are given for %FI.

Block	Stratum	Number of larvae	*Paralabrax* spp.		*Genyonemus lineatus*		*Seriphus politus*	
			Preflexion	Flexion-postflexion	Preflexion	Flexion-postflexion	Preflexion	Flexion-postflexion
A	N	N_t	0	3	25	7	2	0
		N_f	0	1	19	7	2	0
		%FI	—	33.3 ± 70.0	76.0 ± 18.7	100.0 ± 7.1	100.0 ± 25.0	—
	M	N_t	0	0	41	11	49	1
		N_f	0	0	35	11	41	1
		%FI	—	—	85.4 ± 12.0	100.0 ± 4.5	83.7 ± 11.4	100.0 ± 50.0
	E	N_t	1	0	53	185	122	153
		N_f	0	0	50	176	98	117
		%FI	0.0 ± 50.0	—	94.3 ± 7.2	95.1 ± 3.4	80.3 ± 7.5	76.5 ± 7.0
B	N	N_t	0	3	26	1	2	0
		N_f	0	0	17	1	1	0
		%FI	—	0.0 ± 16.7	65.4 ± 20.2	100.0 ± 50.0	50.0 ± 94.3	—
	M	N_t	1	0	41	3	44	3
		N_f	0	0	41	3	29	2
		%FI	0.0 ± 50.0	—	100.0 ± 1.2	100.0 ± 16.7	65.9 ± 15.1	66.7 ± 70.0
	E	N_t	2	1	84	168	45	80
		N_f	0	0	83	153	40	62
		%FI	0.0 ± 25.0	0.0 ± 50.0	98.8 ± 2.9	91.1 ± 4.6	88.9 ± 10.3	77.5 ± 9.8
C	N	N_t	3	6	20	1	12	0
		N_f	0	1	16	1	7	0
		%FI	0.0 ± 16.7	16.7 ± 38.2	80.0 ± 20.0	100.0 ± 50.0	58.3 ± 32.0	—
	M	N_t	8	0	34	10	34	9
		N_f	5	0	29	10	23	8
		%FI	62.5 ± 39.8	—	85.3 ± 13.4	100.0 ± 5.0	67.7 ± 17.2	88.9 ± 26.1
	E	N_t	3	1	83	102	18	36
		N_f	1	0	81	102	12	33
		%FI	33.3 ± 70.0	0.0 ± 50.0	97.6 ± 3.9	100.0 ± 0.5	66.7 ± 24.6	91.7 ± 10.4
D	N	N_t	12	0	9	0	29	0
		N_f	0	0	4	0	11	0
		%FI	0.0 ± 4.2	—	44.4 ± 38.0	—	37.9 ± 19.4	—
	M	N_t	57	1	82	13	41	2
		N_f	3	0	79	13	32	2
		%FI	5.3 ± 6.7	0.0 ± 50.0	96.3 ± 4.7	100.0 ± 3.8	78.0 ± 13.9	100.0 ± 25.0
	E	N_t	5	0	128	50	11	5
		N_f	0	0	126	50	7	4
		%FI	0.0 ± 10.0	—	98.4 ± 2.6	100.0 ± 1.0	63.6 ± 33.0	80.0 ± 45.1
E	N	N_t	2	0	11	0	24	0
		N_f	0	0	10	0	12	0
		%FI	0.0 ± 25.0	—	90.9 ± 21.5	—	50.0 ± 22.1	—
	M	N_t	16	6	20	0	20	0
		N_f	7	5	20	0	17	0
		%FI	43.8 ± 27.4	83.3 ± 38.2	100.0 ± 2.5	—	85.0 ± 18.1	—
	E	N_t	1	3	14	0	0	0
		N_f	0	1	13	0	0	0
		%FI	0.0 ± 50.0	33.3 ± 70.0	92.9 ± 17.0	—	—	—

A and those farther seaward. The Pr larvae contained similar average numbers of prey items per feeding individual in blocks A and B (8.8 and 9.2 items per larva, respectively, summed over the water column), but the FP larvae contained nearly twice as many items in block A as in block B (Table 4).

The diet of the jacksmelt larvae varied little with location or over time: except in March 1979, the principal prey for all larval stages was the small harpacticoid copepod *Euterpina acutifrons*. In the March 1979 survey, the Pr larvae fed almost exclusively on *Labidocera trispinosa* nauplii. *Labidocera trispinosa* nauplii also were an appreciable fraction (36%) of the diet of the older jacksmelt larvae on this survey, although *E. acutifrons* still dominated. Minor components of the diet for the Pr larvae included centric diatoms (*Coscinodiscus* spp.), bivalve veligers, tintinnids (*Stenosomella* spp.), cirriped nauplii, and other copepods, e.g., *Paracalanus parvus* (Table 4). The FP larvae consumed all of these items as well, in addition to cirriped cypris larvae and a wider variety of copepods (e.g., *Oncea*, *Oithona*, *Corycaeus*).

Leuresthes tenuis

Larval grunion were collected almost exclusively from the neuston, in all five cross-shelf blocks, in September and Ocotber 1978 and April through September 1979. In total, 233 specimens were dissected (Table 1); 36% contained prey. Overall, feeding incidence differed little between the Pr stage larvae (39.6 ± 14.9%) and older larvae (35.7 ± 7.2%). The FP larvae displayed a

TABLE 4.—Diet of larval *Atherinopsis californiensis*. Results for preflexion stage larvae are given above; those for flexion-postflexion stage larvae are below. A blank column indicates that no larvae containing food occurred in that stratum. Since larval *A. californiensis* occurred only in the blocks A–C neuston and block A midwater, only those strata are shown. Water column strata are N = neuston; M = midwater. %N = the percent of the total food items attributable to a given category; %FO = the percent of the larvae containing food items that contained prey of the given category. Copepods listed as prey species include both copepodites and adults.

Block:	A (6–9 m)				B (9–12 m)		C (12–22 m)
Stratum:	N		M		N		N
Prey item	%N	%FO	%N	%FO	%N	%FO	%N
Preflexion							
Coscinodiscus spp.	1.4	10.0	0	0	0	0	
Stenosomella spp.	11.0	30.0	15.2	50.0	0	0	
Bivalve veligers	4.1	20.0	0	0	0	0	
Paracalanus parvus	0	0	3.0	50.0	0	0	
Labidocera trispinosa (nauplii)	52.1	40.0	0	0	97.8	100.0	
Euterpina acutifrons	19.2	50.0	27.3	100.0	2.2	20.0	
E. acutifrons (nauplii)	9.6	30.0	54.5	100.0	0	0	
Cirriped nauplii	2.7	20.0	0	0	0	0	
Total food items	73		33		46		0
Mean prey/feeding larva	7.3		16.5		9.2		0
Flexion-Postflexion							
Coscinodiscus spp.	4.7	6.5	0	0	8.1	16.7	
Stenosomella spp.	4.2	9.7	9.1	100.0	0	0	
Bivalve veligers	1.7	12.9	0	0	0	0	
Paracalanus parvus	0.8	6.5	27.3	100.0	0	0	
Labidocera trispinosa (nauplii)	1.7	3.2	0	0	35.1	33.3	
Oithona oculata	0.3	3.2	0	0	0	0	
Oncea spp.	0	0	0	0	2.7	16.7	
Euterpina acutifrons	79.9	80.6	54.5	100.0	40.5	16.7	
E. acutifrons (nauplii)	5.8	6.5	9.1	100.0	5.4	16.7	
Unidentified copepods	0.8	6.5	0	0	5.4	33.3	
Unidentified	0	0	0	0	2.7	16.7	
Total food items	359		11		37		0
Mean prey/feeding larva	11.6		11.0		6.2		0

clear gradient of feeding incidence from highest nearshore to lowest offshore (Table 3). Feeding incidence for the Pr larvae was highest between about 1 and 3.8 km from shore, and lower both seaward and shoreward, with no overlap of confidence limits (Table 3). Both the Pr and FP larvae consumed more items per feeding individual in the most nearshore block than elsewhere (Table 5). This was especially striking for the Pr larvae.

The most important prey for both the Pr and FP larvae was *Euterpina acutifrons* (Table 5). The Pr larvae tended to utilize *E. acutifrons* nauplii only a little less than the copepodites and adults, while the older larvae showed a clear preference for the copepodites and adults (Table 5). *Coscinodiscus* spp. were important in the diet of the Pr larvae, but constituted only a minor fraction of the FP diet. Minor components of the diet for the Pr larvae included dinoflagellates (*Peridinium* spp.), tintinnids (*Stenosomella* spp.), and small copepods (*Paracalanus parvus* and unidentified nauplii). Older larvae also consumed these items, as well as cirriped nauplii, bivalve veligers, and a wider variety of copepods (e.g., *Oncea, Oithona, Microsetella,* and *Corycaeus*).

TABLE 5.—Diet of larval *Leuresthes tenuis*. Results for preflexion stage larvae are given above; those for flexion-postflexion stage larvae are below. A blank column indicates that no larvae containing food occurred in that stratum. Since larval *L. tenuis* occurred only in the neuston and midwater, only those strata are shown. Water column strata are N = neuston; M = midwater. %N = the percent of the total food items attributable to a given category; %FO = the percent of the larvae containing food items that contained prey of the given category. Copepods listed as prey species include both copepodites and adults.

Block:	A (6–9 m)				B (9–12 m)			C (12–22 m)			D (22–45 m)			E (45–75 m)	
Stratum:	N		M		N		M	N		M	N		M	N	M
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%N	%FO	%N	%N	%FO	%N	%N	%N
Preflexion															
Coscinodiscus spp.	33.3	33.3			0	0		0	0						
Peridinium spp.	3.0	33.3			0	0		0	0						
Stenosomella spp.	6.1	33.3			0	0		0	0						
Euterpina acutifrons	36.4	66.7			17.4	30.0		57.1	66.7						
E. acutifrons (nauplii)	18.1	33.3			0	0		0	0						
Unidentified copepods	3.0	33.3			65.2	80.0		0	0						
Unidentified copepod nauplii	0	0			13.0	10.0		0	0						
Unidentified Crustacea	0	0			0	0		28.6	33.3						
Unidentified	0	0			4.3	10.0		14.3	16.7						
Total food items	33		0		23		0	7		0	0		0	0	0
Mean prey/feeding larva	11.0		0		2.3		0	1.2		0	0		0	0	0
Flexion-postflexion															
Coscinodiscus spp.	1.9	10.0	0	0	0	0		0	0		0	0			
Peridinium spp.	0.1	2.1	0	0	0	0		0	0		0	0			
Stenosomella spp.	2.0	10.0	0	0	0	0		0	0		0	0			
Bivalve Veligers	0.1	2.1	0	0	0	0		0	0		0	0			
Acartia tonsa	0	0	100.0	100.0	0	0		0	0		0	0			
Paracalanus parvus	1.4	10.0	0	0	0.8	7.7		0	0		0	0			
Oithona oculata	0	0	0	0	9.2	15.4		0	0		0	0			
Corycaeus anglicus	0.3	2.1	0	0	0	0		0	0		0	0			
Oncea spp.	1.0	6.3	0	0	0	0		0	0		0	0			
Euterpina acutifrons	62.5	66.7	0	0	82.4	76.9		100.0	100.0		100.0	100.0			
E. acutifrons (nauplii)	15.5	37.5	0	0	0	0		0	0		0	0			
Microsetella rosea	0.1	2.1	0	0	0	0		0	0		0	0			
Unidentified copepods	13.2	20.8	0	0	4.2	38.5		0	0		0	0			
Ciiriped nauplii	0.3	4.2	0	0	0	0		0	0		0	0			
Unidentified	1.6	20.8	0	0	3.4	30.8		0	0		0	0			
Total food items	699		1		119		0	21		0	3		0	0	0
Mean prey/feeding larva	14.6		1.0		9.2		0	7.0		0	3.0		0	0	0

Paralichthys californicus

Two hundred and nine larval California halibut were examined from samples collected between September 1978 and February 1979, and in August and September 1979 (Table 1). Most larvae (89%) were Pr stage. The overall 28% feeding incidence was comparable to the 22% nighttime incidence noted in the day/night sample set. Although the feeding incidence for the Pr larvae was nearly 70% higher than that of the FP larvae (29.5 ± 6.9% vs. 17.4 ± 17.7%), it was well within the 95% confidence limits about the FP value. The Pr larvae displayed a higher feeding incidence in the most nearshore block, but only the confidence limits about the %FI values for the most nearshore and seaward blocks failed to overlap (block A: 70.0 ± 33.4%; block E: 11.5 ± 14.2%). The highest feeding incidence for the FP larvae occurred in the 45–75 m depth block, but all confidence limits broadly overlapped owing to the small sample sizes (Table 3). Among the FP larvae, all four specimens that contained food were collected in midwater. Pr larvae in the nearshore blocks typically contained more prey items per individual than did larvae in the most offshore blocks (Table 6).

Larval California halibut consumed few types of prey. Bivalve veligers, *Euterpina acutifrons* nauplii, the tintinnid genus *Stenosomella*, and unidentified material (including unidentified invertebrate eggs, and setae—presumably from polychaete larvae) accounted for most of the diet of the Pr larvae (Table 6). Young larvae consumed a narrower range of prey types near shore than they did farther seaward. Most of the diet near shore was composed of *Stenosomella* spp., while seaward of the 12 m isobath, *Euterpina acutifrons* nauplii, unidentified material, and bivalve veligers constituted the bulk of the diet. The few FP larvae with gut contents contained only unidentifiable material (Table 6).

Paralabrax spp.

Due to the difficulty and uncertainty in separating larval kelp and sand basses, identification was only to the level of genus. A total of 135 larval *Paralabrax* spp. were examined from samples collected between September and November 1978 and between July and Septem-

TABLE 6.—Diet of larval *Paralichthys californicus*. Results for preflexion stage larvae are given above; those for the column strata are N = neuston; M = midwater; E = epibenthos. %N = the percent of the total food items attributable to listed as prey species include both copepodites and adults.

Block:	A (6–9 m)						B (9–12 m)					
Stratum:	N		M		E		N		M		E	
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO
Preflexion												
Rhizosolenia spp.	0	0	0	0	0	0	0	0	0	0	0	0
Peridinium spp.	0	0	0	0	0	0	0	0	0	0	0	0
Radiolaria	0	0	0	0	0	0	0	0	0	0	0	0
Stenosomella spp.	90.9	100.0	90.6	25.0	100.0	100.0	77.3	25.0	98.2	50.0	0	0
Bivalve veligers	9.1	50.0	0	0	0	0	0	0	0	0	0	0
Euterpina acutifrons (nauplii)	0	0	0	0	0	0	0	0	1.8	50.0	0	0
Unidentified copepods	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified nauplii	0	0	0	0	0	0	0	0	0	0	100.0	100.0
Unidentified	0	0	9.4	75.0	0	0	22.7	75.0	0	0	0	0
Total food items	11		32		23		22		55		2	
Mean prey/feeding larva	5.5		8.0		23.0		5.5		27.5		2.0	
Flexion-postflexion												
Unidentified												
Total food item	0		0		0		0		0		0	
Mean prey/feeding larva	0		0		0		0		0		0	

ber 1979, mainly in midwater, seaward of the 12 m isobath (Table 1). Most of the larvae were Pr stage (82%). Eighteen percent of the larvae dissected contained food, similar to the 21% nighttime average noted in the day/night comparison. There was no clear cross-shelf pattern in feeding incidence (Table 3), but a vertical pattern may have been suggested by the lower incidence in the neuston (3.4 ± 8.3%) and higher incidences in midwater (22.5 ± 9.2%) and epibenthos (13.3 ± 20.5%). Although the average feeding incidence for the Pr larvae (14.7 ± 1.1%) was less than half that for the FP larvae (33.3 ± 20.9%), it still was contained within the broad confidence bounds about the FP value.

Tintinnids, bivalve veligers, and copepods were among the most important prey for larval *Paralabrax* spp. (Table 7). Unidentified items (including invertebrate eggs and setae—presumably from polychaete larvae) constituted the major dietary component for the Pr larvae. However, tintinnids (*Stenosomella* spp.) and bivalve veligers also were important. The FP larvae tended to consume larger items, especially copepods (e.g., *Acartia tonsa Euterpina acutifrons*, and *Oithona oculata*). Both the Pr and the FP larvae typically contained few prey items (Table 7).

Genyonemus lineatus

A total of 1,222 larval white croaker were examined from samples collected between October 1978 and June 1979, and in September 1979 (Table 1). Fifty-five percent of the larvae were Pr stage. Nearly all of the larvae contained food: feeding incidence was 92.8% (±2.0%) for the Pr larvae and 95.6% (±1.0%) for the FP larvae. Feeding incidence was high in all strata and all cross-shelf blocks (Table 3). For both larval stage categories, feeding incidence in the neuston was distinctly lower (75.0 ± 4.8%) than it was in midwater (94.5 ± 1.6%) and epibenthos (96.2 ± 0.7%). There was little evidence of a cross-shelf gradient in feeding incidence for either stage category (Table 3).

Larval white croaker consumed a wide variety of prey types (Tables 8, 9). Pr larvae tended to eat smaller items, particularly tintinnids, bivalve and gastropod veligers, and small copepods, especially all stages of *Euterpina acutifrons* (Table 8). The FP larvae consumed these

flexion-postflexion stage larvae are below. A blank column indicates that no larvae contained food occurred in that stratum. Water a given food category; %FO = the percent of larvae containing food items that contained prey of the given category. Copepods

Block:	C (12–22 m)						D (22–45 m)						E (45–75 m)			
Stratum:	N		M		E		N		M		E		N	M		E
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%N	%FO	%N
Preflexion																
Rhizosolenia spp.	0	0	1.7	8.3	0	0	0	0	0	0	0	0		0	0	
Peridinium spp.	0	0	1.7	8.3	0	0	0	0	3.3	9.1	0	0		0	0	
Radiolaria	0	0	0	0	0	0	0	0	3.3	9.1	0	0		0	0	
Stenosomella spp.	0	0	5.0	8.3	0	0	0	0	0	0	0	0		0	0	
Bivalve veligers	0	0	1.7	8.3	8.3	20.0	20.0	50.0	16.7	9.1	50.0	20.0		0	0	
Euterpina acutifrons (nauplii)	0	0	78.3	58.3	50.0	80.0	70.0	75.0	36.7	36.4	20.0	20.0		0	0	
Unidentified copepods	0	0	0	0	16.7	20.0	0	0	0	0	0	0		33.3	33.3	
Unidentified nauplii	0	0	0	0	0	0	0	0	0	0	0	0		0	0	
Unidentified	100.0	100.0	11.7	58.3	25.0	40.0	10.0	25.0	40.0	90.9	30.0	60.0		66.7	66.7	
Total food items	1		60		12		10		30		10		0	3		0
Mean prey/feeding larva	1.0		5.0		2.4		2.5		2.7		2.0		0	1.0		0
Flexion-postflexion																
Unidentified			100.0	100.0										100.0	100.0	
Total food item	0		2		0		0		0		0		0	2		0
Mean prey/feeding larva	0		1.0		0		0		0		0		0	1.0		0

TABLE 7.—Diet of larval *Paralabrax* spp. Results for preflexion stage larvae are given above; those for the flexion-postflexion stage larvae are below. A blank column indicates that no larvae contained food in that stratum. Water column strata are N = neuston; M = midwater; E = epibenthos. %N = the percent of the total food items attributable to a given food category; %FO = the percent of larvae containing food items that contained prey of the given category. Copepods listed as prey include both copepodites and adults.

Block:	A (6–9 m)				B (9–12 m)			C (12–22 m)					
Stratum:	N		M	E	N	M	E	N		M		E	
Prey item	%N	%FO	%N	%N	%N	%N	%N	%N	%FO	%N	%FO	%N	%FO
Preflexion													
Stenosomella spp.										43.8	20.0	0	0
Bivalve veligers										6.3	20.0	0	0
Paracalanus parvus										0	0	0	0
Euterpina acutifrons										12.5	20.0	0	0
E. acutifrons (nauplii)										6.3	20.0	0	0
Unidentified copepods										0	0	0	0
Cirriped nauplii										6.3	20.0	0	0
Unidentified										25.0	80.0	100.0	100.0
Total food items	0	0	0	0	0	0	0	0		16		2	
Mean prey/feeding larva	0	0	0	0	0	0	0	0		3.2		2.0	
Flexion-postflexion													
Acartia tonsa	0	0						100.0	100.0				
Corycaeus anglicus	0	0						0	0				
Oithona oculata	0	0						0	0				
Euterpina acutifrons	0	0						0	0				
Unidentified copepods	0	0						0	0				
Euphausid calyptopis	0	0						0	0				
Unidentified	100.0	100.0						0	0				
Total food items	1	0	0	0	0	0	0	1		0		0	
Mean prey/feeding larva	1.0	0	0	0	0	0	0	1.0		0		0	

Block:	D (22–45 m)				E (45–75 m)				
Stratum:	N	M		E	N	M		E	
Prey item	%N	%N	%FO	%N	%N	%N	%FO	%N	%FO
Preflexion									
Stenosomella spp.		0	0			0	0		
Bivalve veligers		80.0	67.7			9.1	14.3		
Paracalanus parvus		0	0			18.2	14.3		
Euterpina acutifrons		0	0			0	0		
E. acutifrons (nauplii)		0	0			0	0		
Unidentified copepods		20.0	33.3			0	0		
Cirriped nauplii		0	0			0	0		
Unidentified		0	0			72.7	85.7		
Total food items	0	5		0	0	11		0	
Mean prey/feeding larva	0	1.7		0	0	1.6		0	
Flexion-postflexion									
Acartia tonsa						14.3	20.0	0	0
Corycaeus anglicus						0	0	33.3	100.0
Oithona oculata						42.9	20.0	0	0
Euterpina acutifrons						14.3	20.0	33.3	100.0
Unidentified copepods						14.3	20.0	33.3	100.0
Euphausid calyptopis						14.3	20.0	0	0
Unidentified						0	0	0	0
Total food items	0	0		0	0	7		3	
Mean prey/feeding larva	0	0		0	0	1.4		3.0	

small items as well, but in addition consumed larger items such as larger copepod species and mysids (Table 9). Cross-shelf patterns in dietary composition were apparent; for example, tintinnids in the Pr diet shifted from *Stenosomella* spp. near shore to predominantly *Condonaria* spp. farthest from shore (Table 8). Pr larvae also tended to consume more bivalve veligers more frequently in the blocks farthest from shore, but more gastropod veligers nearer shore (Table 8). The FP larvae likewise consumed most gastropod veligers nearer shore, but did not display clear evidence of a cross-shelf pattern in the consumption of bivalve veligers (Table 9). The average number of prey items consumed by the Pr larvae ranged from 2.9 to 8.8 per feeding individual (Table 8), while for the FP larvae the number of items consumed ranged from 2.0 to 8.3 (Table 9). Cross-shelf patterns in the number of items consumed were not apparent. The FP larvae contained more prey items per feeding individual in midwater and epibenthos than in the neuston. There were no consistent differences between strata for the Pr larvae or between midwater and epibenthos samples for the older larvae (Tables 8, 9).

Seriphus politus

A total of 742 larval queenfish (61% Pr stage) were examined from samples collected between September and November 1978 and between March and September 1979 (Table 1). The overall 67% feeding incidence was comparable to the 72% night incidence noted in the day/night sample set. Feeding incidence differed little between the Pr larvae (73.5 ± 4.2%) and the FP larvae (79.2 ± 4.8%). Relatively few larvae were available for dissection from the neuston samples, and overall these larvae displayed the lowest feeding incidence (48.5 ± 12.6% for the Pr larvae; no FP larvae occurred in the neuston). Feeding incidence differed little between midwater (76.4 ± 6.1%) and epibenthos (79.4 ± 3.8%). The feeding incidence for the Pr larvae was highest in block A (81.5 ± 6.1%) where larval abundance was highest, and ranged between about 62 and 68% in the remaining blocks. Confidence limits about the means for blocks B (63.1 ± 9.4%) and D (61.7 ± 11.2%) did not overlap the confidence limits about the mean for block A, but those about the means for blocks C (66.7 ± 12.4%) and E (65.9 ± 15.1%) did overlap the confidence limits about the block A mean. The lowest feeding incidences for the FP larvae occurred in blocks A (76.6 ± 7.0%) and B (77.1 ± 9.6%) where larval abundance was highest, and the highest feeding incidences occurred in blocks C (91.1 ± 9.4%) and D (85.7 ± 33.1%) where larval abundance was low. However, the confidence bounds about these estimates overlapped in all cases.

Larval queenfish consumed a wide variety of prey types (Tables 10, 11). Pr larvae consumed mainly small items, especially bivalve veligers and small copepods such as *Paracalanus parvus* and *Euterpina acutifrons* (Table 10). The FP larvae also consumed these small items in addition to larger items, especially mysids and gammarid amphipods (Table 11). Cross-shelf patterns in dietary composition and number of items consumed were not clear. For the Pr larvae, feeding specimens contained fewer prey items per individual in block E than elsewhere (Table 10), but for the FP larvae no pattern was apparent (Table 11). Both the Pr and FP larvae tended to consume slightly more prey items per feeding individual in midwater than in epibenthos. Smaller prey contributed larger fractions of the diet in midwater than in the epibenthos for both larval stage classes.

DISCUSSION

Both the limited day/night sample series and the much larger night-only sample set indicated that larvae contained food well into the night. A nonzero feeding incidence does not necessarily imply recent feeding, however, but only indicates the presence of food in the gut. For example, a slow digestion and evacuation rate might result in the appearance of nocturnal feeding even if the larvae in fact were not feeding. On the other hand, a low feeding incidence does not necessarily imply nonfeeding, especially for taxa that have a straight gut, since these larvae frequently void their gut contents during capture and fixation (June and Carlson 1971; Hay 1981). Hunter (1981) noted that fish larvae are visual feeders lacking rods and retinomotor pigment migration (e.g., Blaxter 1968) and are probably largely restricted to feeding in daylight hours. The low feeding incidences noted for larval *Paralabrax* spp. in the night samples suggests that they do feed only during the day. Similarly, *Paralichthys californicus* larvae may feed only during the day, although their day-night differences in feeding incidence were smaller and less convincing owing to the broad confidence limits about the %FI values. Both

TABLE 8.—Diet of preflexion stage larvae of *Genyonemus lineatus*. A blank column
N = neuston; M = midwater; E = epibenthos. %N = the percent of the total foo
containing food items that contained prey of the given category. Copepods listed

Block:	A (6–9 m)						
Stratum:	N		M		E		
Prey item	%N	%FO	%N	%FO	%N	%FO	%
Coscinodiscus spp.	0	0	0	0	0	0	
Peridinium spp.	3.8	10.5	0.7	2.9	0	0	
Radiolaria	0	0	0	0	0	0	
Stenosomella spp.	37.7	10.5	43.3	25.7	4.4	8.0	2
Condonaria spp.	0	0	0	0	0	0	
Bivalve veligers	6.6	26.3	4.6	17.1	3.2	8.0	1
Gastropod veligers	2.8	15.8	1.3	8.6	0.6	2.0	
Spionidae	0	0	0	0	0	0	
Polychaete trochophores	0	0	0.3	2.9	5.7	18.0	
Cyphonautes, uniden.	0	0	0	0	0	0	
Penilia avirostris	0	0	0	0	0	0	
Cladocerans, uniden.	0	0	0	0	0	0	
Paracalanus parvus	0	0	3.9	17.1	10.1	18.0	
Oithona oculata	0	0	1.0	8.6	1.3	4.0	
O. oculata nauplii	0	0	0	0	0	0	
Corycaeus anglicus	0	0	0	0	1.3	4.0	
Oncea spp.	0	0	0.3	2.9	0	0	
Euterpina acutifrons	16.1	36.8	18.9	60.0	27.8	48.0	1
E. acutifrons nauplii	6.6	15.8	13.0	28.6	7.6	12.0	1
Microsetella rosea	0	0	0.3	2.9	0	0	5
M. rosea nauplii	0	0	0	0	0	0	
Longipedia spp. nauplii	1.9	10.5	0	0	0	0	
Copepods, unidentified	0	0	0	0	12.7	18.0	
Copepod nauplii, uniden.	0	0	0	0	0.6	2.0	
Ostracods, uniden.	0	0	0	0	0	0	
Cumaceans, uniden.	0	0	0	0	0	0	
Euphausids, calyptopis	0	0	0	0	0	0	
Unidentified	24.5	78.9	12.4	60.0	24.6	46.0	1
Total food items	106		307		158		7
Mean prey/feeding larva	5.6		8.8		3.2		

olumn indicates that no larvae contained food in that stratum. Water column strata are
al food items attributable to a given food category; %FO = the percent of the larvae
listed as prey species include both copepodites and adults.

	B (9–12 m)						C (12–22 m)					
	N		M		E		N		M		E	
FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO
	0	0	0	0	0.6	2.4	0	0	0	0	0.9	4.9
	1.3	5.9	2.0	9.8	0.1	1.2	0	0	3.6	10.3	1.1	4.9
	0	0	0	0	0	0	0	0	0	0	0	0
.0	21.8	23.5	18.1	24.4	0.6	1.2	0	0	0.7	3.4	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
.0	12.8	35.3	8.3	31.7	7.5	20.5	5.4	6.3	3.6	13.8	9.4	24.7
.0	3.8	17.6	3.1	7.3	1.7	6.0	0	0	1.5	6.9	1.1	6.2
	0	0	0	0	0.3	1.2	0	0	0	0	0	0
.0	0	0	0.4	2.4	0.6	2.4	1.8	6.3	1.5	6.9	1.1	6.2
	0	0	0	0	0.6	1.2	0	0	0	0	0.2	1.2
	0	0	0	0	0	0	0	0	0	0	0	0
	1.3	5.9	0	0	0	0	0	0	0	0	0	0
.0	0	0	0.4	2.4	1.7	7.2	0	0	0	0	1.1	4.9
.0	1.3	5.9	0	0	5.8	14.5	0	0	2.2	3.4	2.5	6.2
	0	0	0.4	2.4	1.7	6.0	0	0	2.2	6.9	0.9	4.9
.0	0	0	0.4	2.4	0.9	3.6	0	0	0	0	6.2	16.0
	0	0	0	0	0.9	3.6	0	0	1.5	3.4	3.9	4.9
.0	17.9	35.3	15.7	61.0	38.9	42.2	5.4	18.8	24.1	44.8	32.5	64.2
.0	15.4	23.5	25.2	39.0	2.9	9.6	46.4	50.0	17.5	34.5	12.1	29.6
	5.1	17.6	3.9	14.6	3.5	8.4	0	0	9.5	20.7	10.5	19.8
	0	0	0.8	4.9	0	0	0	0	0	0	0.2	1.2
	3.8	11.8	3.1	9.8	0	0	3.6	12.5	2.9	10.3	1.6	8.6
.0	0	0	0.8	2.4	5.2	9.6	3.6	6.3	2.9	10.3	1.6	4.9
.0	0	0	0	0	0	0	0	0	0	0	0.5	1.2
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
.0	15.4	58.8	17.3	48.8	26.5	55.4	33.9	68.8	26.3	58.6	12.4	44.4
	78		254		347		56		137		437	
	4.6		6.2		4.2		3.5		4.7		5.4	

TABLE 8.—*Continued.*

Block:	D (22–45 m)						
Stratum:	N		M		E		
Prey item	%N	%FO	%N	%FO	%N	%FO	%N
Coscinodiscus spp.	0	0	1.0	3.8	0.9	2.4	0
Peridinium spp.	0	0	8.0	13.9	0.6	2.4	6.9
Radiolaria	0	0	0.5	1.3	0	0	0
Stenosomella spp.	0	0	0	0	0	0	0
Condonaria spp.	0	0	1.5	5.1	0	0	24.1
Bivalve veligers	22.7	25.0	40.5	62.0	19.4	35.7	24.1
Gastropod veligers	0	0	0.8	3.8	1.2	5.6	0
Spionidae	0	0	0	0	0	0	0
Polychaete trochophores	0	0	0	0	0.6	3.2	0
Cyphonautes, uniden.	0	0	0.5	2.5	0.5	1.6	0
Penilia avirostris	0	0	0	0	0.2	0.8	0
Cladocerans, uniden.	0	0	0	0	0	0	0
Paracalanus parvus	0	0	0	0	0.5	2.4	0
Oithona oculata	0	0	0	0	2.9	9.5	0
O. oculata nauplii	4.5	25.0	1.5	7.6	0	0	0
Corycaeus anglicus	0	0	0.5	2.5	1.7	5.6	0
Oncea spp.	0	0	1.5	5.1	0.8	3.2	0
Euterpina acutifrons	4.5	25.0	21.6	39.2	57.9	80.2	0
E. acutifrons nauplii	13.6	50.0	10.3	22.8	1.2	4.0	3.4
Microsetella rosea	13.6	25.0	5.0	16.5	3.5	9.5	0
M. rosea nauplii	0	0	0	0	0	0	13.8
Longipedia spp. nauplii	22.7	25.0	0	0	0	0	3.4
Copepods, unidentified	0	0	0	0	0.6	2.4	0
Copepod nauplii, uniden.	0	0	0.5	1.3	0	0	3.4
Ostracods, uniden.	0	0	0	0	0.2	0.8	0
Cumaceans, uniden.	0	0	0	0	0.2	0.8	0
Euphausids, calyptopis	0	0	0	0	0.5	2.4	0
Unidentified	18.2	50.0	6.3	15.2	6.6	23.8	20.7
Total food items	22		398		648		29
Mean prey/feeding larva	5.5		5.0		5.1		2.9

E (45–75 m)					
N		M		E	
%N	%FO	%N	%FO	%N	%FO
0	0	0	0	0	0
6.9	10.0	6.4	25.0	0	0
0	0	0	0	0	0
0	0	3.8	5.0	3.6	7.7
24.1	30.0	5.1	20.0	0	0
24.1	50.0	19.2	60.0	16.4	38.5
0	0	0	0	0	0
0	0	0	0	0	0
0	0	2.6	10.0	1.8	7.7
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	3.8	10.0	3.6	15.4
0	0	0	0	1.8	7.7
3.4	10.0	5.1	10.0	0	0
0	0	2.6	10.0	0	0
13.8	40.0	2.6	10.0	5.5	15.4
3.4	10.0	0	0	0	0
0	0	1.3	5.0	0	0
3.4	10.0	1.3	5.0	0	0
0	0	0	0	1.8	7.7
0	0	0	0	0	0
0	0	0	0	0	0
20.7	60.0	46.2	65.0	65.5	61.5
29		78		55	
2.9		3.9		4.2	

TABLE 9.—Diet of flexion-postflexion stage larvae of *Genyonemus lineatus*. Since none of these larvae occurred in block Water column strata are N = neuston; M = midwater; E = epibenthos. %N = the percent of the total food items the given category. Copepods listed as prey include both copepodites and adults.

Block:	A (6–9 m)						B (9–12 m)					
Stratum:	N		M		E		N		M		E	
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO
Coscinodiscus spp.	0	0	0	0	0.2	0.6	0	0	6.3	33.3	0	0
Rhizosolenia spp.	0	0	0	0	0.1	0.6	0	0	0	0	0	0
Peridinium spp.	0	0	0	0	0	0	0	0	0	0	0	0
Radiolaria	0	0	0	0	0	0	0	0	0	0	0	0
Sagitta spp.	0	0	0	0	0.4	1.1	0	0	0	0	0.2	1.3
Bivalve veligers	6.3	14.3	9.1	63.6	2.3	7.4	0	0	0	0	5.8	19.0
Gastropod veligers	12.5	28.6	1.3	9.1	0.5	2.3	0	0	0	0	1.9	5.2
Spionidae	6.3	14.3	1.3	9.1	0.5	2.3	0	0	0	0	0	0
Polychaete larvae	0	0	9.1	27.3	2.3	5.7	0	0	6.3	33.3	9.5	26.1
Membranipora spp. cyphonautes	0	0	0	0	0.1	0.6	0	0	0	0	0.1	0.7
Cyphonautes, uniden.	0	0	0	0	0.8	4.0	0	0	0	0	1.0	3.9
Penilia avirostris	0	0	0	0	0.2	1.1	0	0	0	0	0	0
Acartia tonsa	0	0	0	0	0.1	0.6	0	0	0	0	2.1	9.8
Paracalanus parvus	37.5	28.6	32.5	63.6	54.1	48.9	0	0	18.8	66.7	29.5	51.0
Labidocera trispinosa	0	0	1.3	9.1	4.5	9.7	0	0	12.5	33.3	1.2	4.6
Pontellopsis spp.	0	0	0	0	0	0	0	0	0	0	2.6	7.8
Candacia spp.	0	0	0	0	0	0	0	0	0	0	0	0
Oithona oculata	0	0	3.9	27.3	1.1	3.4	0	0	0	0	0.6	2.6
O. oculata nauplii	0	0	0	0	0	0	0	0	0	0	0	0
O. plumifera	0	0	0	0	0	0	0	0	0	0	0.2	1.3
Corycaeus anglicus	0	0	2.6	9.1	0.6	2.3	0	0	0	0	1.1	5.9
Oncea spp.	0	0	0	0	0.2	1.1	0	0	0	0	0.3	2.0
Euterpina acutifrons	18.8	42.9	31.2	81.8	12.0	30.1	0	0	50.0	100.0	30.3	54.2
E. acutifrons nauplii	6.3	14.3	0	0	1.7	6.3	0	0	0	0	0.2	1.3
Microsetella rosea	0	0	0	0	0.1	0.6	0	0	0	0	0.3	2.0
Longipedia spp. nauplii	0	0	0	0	0.1	0.6	0	0	0	0	0	0
Copepods, uniden.	0	0	0	0	11.3	32.4	0	0	0	0	4.3	14.4
Copepod nauplii, uniden.	6.3	14.3	1.3	9.1	0	0	0	0	0	0	0	0
Cirriped nauplii	0	0	0	0	0.1	0.6	0	0	0	0	0.5	2.0
Cirriped cypris	0	0	0	0	0.1	0.6	0	0	0	0	0.2	1.3
Nebalia spp.	0	0	1.3	9.1	0	0	0	0	0	0	0.1	0.7
Ostracods, uniden.	0	0	0	0	0	0	0	0	0	0	0.1	0.7
Metamysidopsis elongata	0	0	0	0	0	0	0	0	0	0	0.1	0.7
Mysidopsis californica	0	0	0	0	0	0	0	0	0	0	0.3	2.0
M. intii	0	0	0	0	0	0	0	0	0	0	0.2	0.7
Neomysis rayii	0	0	0	0	0	0	0	0	0	0	0.3	2.0
Neomysis spp. juveniles	0	0	0	0	1.4	5.1	0	0	0	0	0.3	1.3
Siriella pacifica	0	0	0	0	0	0	0	0	0	0	0.1	0.7
Mysids, uniden.	0	0	0	0	0.8	2.3	0	0	0	0	0.7	3.9
Gammarids, uniden.	0	0	0	0	1.4	5.7	0	0	0	0	0.3	2.0
Euphausids, calyptopis	0	0	0	0	0.1	0.6	0	0	0	0	0	0
Caridean zoeae	0	0	0	0	0.1	0.6	0	0	0	0	0	0
Brachyuran zoeae	0	0	0	0	0	0	0	0	0	0	0.1	0.7
Brachyuran megalopae	0	0	0	0	0.1	0.6	0	0	0	0	0	0
Fish larvae	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified	6.3	14.3	5.2	27.3	2.6	9.1	100.0	100.0	6.3	33.3	5.0	24.8
Total food items	16		77		844		2		16		884	
Mean prey/feeding larva	2.3		7.0		4.8		2.0		5.3		5.8	

E, that block is not included on the table. A blank column indicates that no larvae contained food in that stratum. attributable to a given food category; %FO = the percent of the larvae containing food items that contained prey of

Block:	C (22–45 m)						D (45–75 m)				
Stratum:	N		M		E		N	M		E	
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%N	%FO	%N	%FO
Coscinodiscus spp.	0	0	0	0	0.5	2.9		0	0	0.6	4.0
Rhizosolenia spp.	0	0	0	0	0	0		0	0	0	0
Peridinium spp.	0	0	0	0	0.6	2.0		0	0	0.3	2.0
Radiolaria	0	0	0	0	0.1	1.0		0	0	0	0
Sagitta spp.	0	0	0	0	0	0		0	0	0.3	2.0
Bivalve veligers	0	0	7.4	30.0	2.1	12.7		6.2	23.1	4.5	22.0
Gastropod veligers	0	0	3.7	20.0	1.2	9.8		0	0	2.9	18.0
Spionidae	0	0	0	0	0	0		0	0	0.3	2.0
Polychaete larvae	0	0	0	0	6.1	25.5		0	0	0.3	2.0
Membranipora spp. cyphonautes	0	0	0	0	0	0		0	0	0	0
Cyphonautes, uniden.	0	0	0	0	0.5	2.0		0	0	0.3	2.0
Penilia avirostris	0	0	0	0	0	0		0	0	0	0
Acartia tonsa	0	0	0	0	0	0		0	0	0	0
Paracalanus parvus	0	0	7.4	30.0	18.0	37.3		0	0	1.9	6.0
Labidocera trispinosa	0	0	0	0	0	0		0	0	0	0
Pontellopsis spp.	0	0	0	0	4.0	18.6		0	0	0	0
Candacia spp.	0	0	1.9	10.0	0	0		0	0	0	0
Oithona oculata	0	0	9.3	10.0	0.7	5.9		4.9	7.7	4.2	10.0
O. oculata nauplii	0	0	0	0	0.2	2.0		1.2	7.7	0	0
O. plumifera	0	0	1.9	10.0	0	0		0	0	0	0
Corycaeus anglicus	0	0	1.9	10.0	6.3	28.4		1.2	7.7	4.2	16.0
Oncea spp.	0	0	27.8	50.0	15.2	33.3		2.5	7.7	1.0	4.0
Euterpina acutifrons	33.3	100.0	29.6	40.0	31.4	61.8		65.4	92.3	70.2	86.0
E. acutifrons nauplii	0	0	0	0	0	0		9.9	15.4	0.3	2.0
Microsetella rosea	0	0	3.7	20.0	2.4	12.7		1.2	7.7	1.6	8.0
Longipedia spp. nauplii	0	0	0	0	0	0		0	0	0	0
Copepods, uniden.	66.7	100.0	0	0	1.3	4.9		0	0	2.9	10.0
Copepod nauplii, uniden.	0	0	0	0	3.8	2.0		0	0	0	0
Cirriped nauplii	0	0	0	0	0	0		0	0	0	0
Cirriped cypris	0	0	0	0	0	0		0	0	0	0
Nebalia spp.	0	0	0	0	0	0	0	0	0	0	0
Ostracods, uniden.	0	0	0	0	0	0	0	0	0	0.3	2.0
Metamysidopsis elongata	0	0	0	0	0	0	0	0	0	0	0
Mysidopsis californica	0	0	0	0	0	0		0	0	0	0
M. intii	0	0	0	0	0	0		0	0	0	0
Neomysis rayii	0	0	0	0	0.5	3.9		0	0	1.0	6.0
Neomysis spp. juveniles	0	0	0	0	0	0		0	0	0	0
Siriella pacifica	0	0	0	0	0	0		0	0	0	0
Mysids, uniden.	0	0	0	0	0	0		0	0	0	0
Gammarids, uniden.	0	0	0	0	0	0		0	0	0	0
Euphausids, calyptopis	0	0	0	0	0.2	2.0		1.2	7.7	0	0
Caridean zoeae	0	0	0	0	0.2	2.0		0	0	0	0
Brachyuran zoeae	0	0	0	0	0.1	1.0		0	0	0	0
Brachyuran megalopae	0	0	0	0	0	0		0	0	0	0
Fish larvae	0	0	0	0	0.1	1.0		0	0	0	0
Unidentified	0	0	5.6	20.0	4.0	25.5		6.2	23.1	2.6	14.0
Total food items	3		54		846		0	81		309	
Mean prey/feeding larva	3.0		5.4		8.3		0	6.2		6.2	

TABLE 10.—Diet of preflexion stage larvae of *Seriphus politus*. A blank column indica
N = neuston; M = midwater; E = epibenthos. %N = the percent of the total food ite
containing food items that contained prey of the given category. Copepods listed as

Block:	A (6–9 m)							
Stratum:	N		M		E		N	
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	
Radiolaria	0	0	0	0	0	0	0	
Stenosomella spp.	0	0	0	0	0	0	0	
Condonaria spp.	0	0	0	0	0	0	0	
Tintinnids, uniden.	0	0	4.2	7.3	0	0	0	
Bivalve veligers	7.7	50.0	7.1	19.5	3.0	8.2	0	
Gastropod veligers	0	0	1.8	7.3	1.7	4.1	0	
Polychaete larvae	0	0	0	0	0	0	0	
Evadne nordmanni	0	0	0	0	0	0	0	
Acartia tonsa	0	0	0	0	0.3	1.0	0	
Paracalanus parvus	0	0	6.5	22.0	17.2	31.6	0	
Oithona oculata	0	0	5.4	4.9	8.9	14.3	0	
O. plumifera	0	0	0	0	0	0	0	
Corycaeus anglicus	0	0	0	0	0	0	0	
Euterpina acutifrons	0	0	56.0	75.6	46.8	55.1	0	
E. acutifrons nauplii	69.2	50.0	4.8	14.6	0.6	2.0	0	
Microsetella rosea	0	0	0	0	0	0	0	
M. rosea nauplii	0	0	0	0	0	0	0	
Copepods, uniden.	0	0	1.8	7.3	10.0	23.5	0	
Copepod nauplii, uniden.	0	0	0	0	0	0	0	
Longipedia spp. nauplii	15.4	100.0	1.8	7.3	0	0	0	
Holmesimysis costata	0	0	0	0	0	0	0	
Neomysis spp., juveniles	0	0	0	0	0.3	1.0	0	
Mysids, uniden.	0	0	0	0	0.6	2.0	0	
Cumaceans, uniden.	0	0	0	0	0	0	0	
Gammarids, uniden.	0	0	0	0	0.8	3.1	0	
Crustaceans, uniden.	0	0	0	0	0	0	0	
Unidentified	7.7	50.0	10.7	43.9	10.0	35.7	100.0	
Total food items	13		168		361		1	
Mean prey/feeding larva	6.5		4.1		3.7		1.0	

indicates that no larvae contained food in that stratum. Water column strata are
ood items attributable to a given food category; %FO = the percent of the larvae
sted as prey include both copepodites and adults.

B (9–12 m)						C (12–22 m)					
N		M		E		N		M		E	
%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO
0	0	0	0	0	0	0	0	0	0	0	0
0	0	20.0	10.3	0	0	20.5	14.3	12.3	13.0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	1.4	3.4	0	0	0	0	0	0	0	0
0	0	2.9	3.4	1.5	7.5	7.7	28.6	8.6	30.4	4.8	16.7
0	0	1.4	3.4	0.5	2.5	0	0	0	0	2.4	8.3
0	0	1.4	3.4	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	2.5	8.7	0	0
0	0	4.3	10.3	5.4	25.0	0	0	0	0	2.4	8.3
0	0	5.7	3.4	1.5	7.5	2.6	14.3	22.2	17.4	0	0
0	0	0	0	0.5	2.5	0	0	0	0	2.4	8.3
0	0	0	0	0	0	0	0	0	0	2.4	8.3
0	0	41.4	69.0	69.8	82.5	5.1	14.3	6.2	21.7	45.2	33.3
0	0	2.9	6.9	0.5	2.5	41.0	28.6	21.0	21.7	11.9	33.3
0	0	0	0	1.0	5.0	0	0	0	0	0	0
0	0	0	0	0	0	2.6	14.3	0	0	0	0
0	0	7.1	13.8	3.9	17.5	5.1	28.6	7.4	21.7	7.1	16.7
0	0	0	0	0	0	0	0	2.5	8.7	0	0
0	0	0	0	0	0	0	0	4.9	8.7	0	0
0	0	0	0	0	0	0	0	0	0	2.4	8.3
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0.5	2.5	0	0	0	0	0	0
0	0	0	0	0.5	2.5	0	0	0	0	2.4	8.3
0	0	0	0	0	0	0	0	0	0	7.1	16.7
0	0	0	0	0	0	0	0	0	0	0	0
00.0	100.0	11.4	27.6	14.6	75.0	15.4	57.1	12.3	43.5	9.5	33.3
1		70		205		39		81		42	
1.0		2.4		5.1		5.6		3.5		3.5	

TABLE 10.—*Continued.*

Block:	D (22–45 m)				
Stratum:	N		M		E
Prey item	%N	%FO	%N	%FO	%N
Radiolaria	0	0	0	0	0
Stenosomella spp.	0	0	14.2	18.8	0
Condonaria spp.	0	0	1.5	6.3	0
Tintinnids, uniden.	0	0	0	0	0
Bivalve veligers	12.1	18.2	25.4	37.5	0
Gastropod veligers	0	0	0.7	3.1	0
Polychaete larvae	3.0	9.1	0	0	0
Evadne nordmanni	0	0	0.7	3.1	0
Acartia tonsa	0	0	0.7	3.1	0
Paracalanus parvus	12.1	18.2	1.5	6.3	0
Oithona oculata	0	0	20.9	21.9	5.9
O. plumifera	0	0	0	0	0
Corycaeus anglicus	0	0	0	0	0
Euterpina acutifrons	27.3	18.2	5.2	18.8	5.9
E. acutifrons nauplii	0	0	1.5	6.3	5.9
Microsetella rosea	0	0	0	0	0
M. rosea nauplii	0	0	0	0	0
Copepods, uniden.	18.2	36.4	5.2	18.8	41.2
Copepod nauplii, uniden.	3.0	9.1	0	0	17.6
Longipedia spp. nauplii	0	0	0	0	0
Holmesimysis costata	0	0	0	0	0
Neomysis spp., juveniles	0	0	0	0	0
Mysids, uniden.	0	0	0.7	3.1	0
Cumaceans, uniden.	0	0	0	0	0
Gammarids, uniden.	0	0	0	0	0
Crustaceans, uniden.	0	0	0	0	0
Unidentified	24.2	54.5	21.6	40.6	23.5
Total food items	33		134		17
Mean prey/feeding larva	3.0		4.2		2.4

		E (45–75 m)				
E		N		M		E
%N	%FO	%N	%FO	%N	%F	%N
0	0	0	0	3.0	5.9	
0	0	42.9	16.7	12.1	11.8	
0	0	0	0	0	0	
0	0	0	0	0	0	
0	0	0	0	27.3	29.4	
0	0	0	0	0	0	
0	0	0	0	0	0	
0	0	0	0	0	0	
0	0	0	0	0	0	
0	0	0	0	0	0	
5.9	14.3	0	0	3.0	5.9	
0	0	0	0	0	0	
0	0	0	0	0	0	
5.9	14.3	4.8	8.3	0	0	
5.9	14.3	0	0	3.0	5.9	
0	0	0	0	0	0	
0	0	0	0	0	0	
41.2	42.9	0	0	0	0	
17.6	14.3	0	0	6.1	11.8	
0	0	0	0	0	0	
0	0	0	0	0	0	
0	0	0	0	0	0	
0	0	0	0	0	0	
0	0	0	0	0	0	
0	0	0	0	0	0	
0	0	4.8	8.3	0	0	
23.5	57.1	47.6	83.3	45.5	54.7	
17		21		33		0
2.4		1.8		1.9		0

TABLE 11.—Diet of flexion-postflexion stage larvae of *Seriphus politus*. A blank column indicates that no column strata are N = neuston; M = midwater; E = epibenthos. %N = the percent of the total food items prey of the given category. Copepods listed as prey include both copepodites and adults.

Block:	A (6–9 m)					B (9–12 m)				
Stratum:	N	M		E		N	M		E	
Prey item	%N	%N	%FO	%N	%FO	%N	%N	%FO	%N	%FO
Sagitta spp.		0	0	0.5	0.9		0	0	0.6	1.6
Bivalve veligers		0	0	0.5	0.9		0	0	0	0
Gastropod veligers		0	0	0	0		0	0	0.6	1.6
Polychaete larvae		0	0	2.6	4.3		0	0	3.1	8.1
Cyphonautes, uniden.		0	0	0	0		0	0	0	0
Evadne nordmanni		0	0	0	0		20.0	50.0	0	0
Acartia tonsa		0	0	8.3	8.5		0	0	3.7	9.7
Paracalanus parvus		0	0	1.6	2.6		0	0	12.3	14.5
Labidocera trispinosa		0	0	0	0		0	0	0.6	1.6
Pontellopsis spp.		0	0	3.6	4.3		0	0	0	0
Oithona oculata		50.0	100.0	1.0	1.7		0	0	0	0
Corycaeus anglicus		0	0	0.5	0.9		0	0	0	0
Oncea spp.		0	0	1.0	0.9		0	0	0	0
Euterpina acutifons		0	0	14.6	13.7		20.0	50.0	32.5	25.8
Microsetella rosea		0	0	0.5	0.9		0	0	0	0
Copepods, uniden.		0	0	9.4	9.4		60.0	100.0	9.8	11.3
Cirriped nauplii		0	0	0	0		0	0	0.6	1.6
Holmesimysis costata		0	0	4.2	6.0		0	0	0.6	1.6
Metamysidopsis elongata		0	0	2.6	3.4		0	0	0	0
Neomysis rayii		0	0	4.2	6.8		0	0	4.9	12.9
Siriella pacifica		0	0	0	0		0	0	1.2	1.6
Mysids, uniden.		12.5	100.0	14.6	19.7		0	0	11.7	25.8
Gammarids, uniden.		12.5	100.0	18.2	22.2		0	0	5.5	14.5
Caridean zoeae		0	0	3.1	5.1		0	0	0.6	1.6
Callianassa spp. zoeae		0	0	0	0		0	0	1.2	3.2
Crustaceans, uniden.		0	0	2.6	4.3		0	0	0.6	1.6
Unidentified		25.0	100.0	6.3	10.3		0	0	9.8	24.2
Total food items	0	8		192		0	5		163	
Mean prey/feeding larva	0	8.0		1.6		0	2.5		2.6	

taxa develop a coil in the gut during the preflexion stage, reducing the likelihood that the low night feeding incidences reflected voiding of the gut contents during capture. The *Paralabrax* spp. feeding incidence was relatively high in the day samples, further suggesting that voiding of the gut contents did not contribute appreciably to the low feeding incidence observed at night.

The higher night feeding incidences for the remaining species, especially *Genyonemus lineatus* and *Seriphus politus*, suggest that they may have continued to feed after dark, at least during the early evening hours. Bagarinao and Hunter (1983) noted that older (≥10 mm) *Engraulis mordax* larvae feed in the dark if prey densities are high enough, and suggested that the full moon provides sufficient illumination for these larvae to feed near the surface at lower prey densities. Other reports of apparent larval fish feeding at night include, for example, Brewer and Kleppel's (1986) report of high feeding incidence until midnight for larval *G. lineatus* collected near shore in Santa Monica Bay, and the reports of Sumida and Moser (1980) and Jenkins (1987) that larval *Merluccius productus* off southern California and *Rhombosolea tapirina* in Port Phillip Bay, Australia, respectively, had high feeding incidences throughout much of the day and night. Brewer and Kleppel (1986) and Sumida and Moser (1980) attributed the high night feeding incidences in their studies to slow digestion rather than to nocturnal feeding, and this cannot be discounted as an alternative explanation for the high nocturnal feeding incidences noted in the present study. This alternative interpretation may be supported by the observation that feeding incidences tended to be lower during the August and September 1979

larvae contained food in that stratum. Block E is not shown because no larvae occurred there. Water attributable to a given food category; %FO = the percent of the larvae containing food items that contained

Block:	C (12–22 m)					D (22–45 m)				
Stratum:	N	M		E		N	M		E	
Prey item	%N	%N	%FO	%N	%FO	%N	%N	%FO	%N	%FO
Sagitta spp.		0	0	0	0		0	0	0	0
Bivalve veligers		0	0	0	0		0	0	0	0
Gastropod veligers		0	0	0	0		0	0	0	0
Polychaete larvae		0	0	0	0		0	0	0	0
Cyphonautes, uniden.		0	0	1.9	3.0		0	0	0	0
Evadne nordmanni		0	0	0	0		0	0	0	0
Acartia tonsa		52.6	50.0	11.1	12.1		0	0	0	0
Paracalanus parvus		0	0	1.9	3.0		0	0	0	0
Labidocera trispinosa		0	0	7.4	9.0		0	0	0	0
Pontellopsis spp.		0	0	1.9	3.0		0	0	0	0
Oithona oculata		0	0	0	0		0	0	0	0
Corycaeus anglicus		0	0	3.7	6.0		0	0	0	0
Oncea spp.		0	0	0	0		0	0	0	0
Euterpina acutifons		0	0	5.6	9.0		0	0	0	0
Microsetella rosea		0	0	0	0		0	0	0	0
Copepods, uniden.		15.8	25.0	5.6	6.0		100.0	100.0	0	0
Cirriped nauplii		0	0	0	0		0	0	0	0
Holmesimysis costata		0	0	5.6	9.0		0	0	0	0
Metamysidopsis elongata		0	0	1.9	3.0		0	0	0	0
Neomysis rayii		0	0	1.9	3.0		0	0	0	0
Siriella pacifica		0	0	0	0		0	0	0	0
Mysids, uniden.		15.8	37.5	13.0	21.2		0	0	25.0	25.0
Gammarids, uniden.		15.8	25.0	27.8	24.2		0	0	25.0	25.0
Caridean zoeae		0	0	0	0		0	0	0	0
Callianassa spp. zoeae		0	0	0	0		0	0	0	0
Crustaceans, uniden.		0	0	0	0		0	0	0	0
Unidentified		0	0	11.1	18.2		0	0	50.0	50.0
Total food items	0	19		54		0	6		4	
Mean prey/feeding larva	0	2.4		1.6		0	3.0		1.0	

surveys. In both cases, sampling was mainly after midnight, in contrast to all other surveys when sampling was mainly before midnight. The potential influence of moonlight on feeding incidence could not be addressed in this study, since all samples were collected within five days of new moon. However, as noted above, the study by Bagarinao and Hunter (1983) suggests that nocturnal feeding is possible during full moon, at least near the surface.

Cross-shelf differences in feeding incidence were apparent for 5 of the 12 stage-taxon categories examined; for 4 of these, feeding incidence was higher near shore and lower in seaward blocks. This may reflect a higher level of feeding intensity near shore, but since the nearshore blocks were always sampled earlier than the offshore blocks during each survey, the alternative explanation that these patterns merely reflected the cessation of larval feeding at night cannot be dismissed. The results for *Atherinopsis californiensis*, and perhaps for *Leuresthes tenuis*, are more likely to represent real, but small-scale differences in feeding incidence since these two species were collected mainly in the two or three shallowest blocks, and relatively little time elapsed between samples.

The composition of the larval diets described in this study is similar to the diet described for many larval marine teleosts (e.g., Arthur 1976; Sumida and Moser 1980; Hunter 1981) in that major fractions were contributed by copepod nauplii and copepodites. In the present study, the harpacticoid copepod *Euterpina acutifrons* was an important component of the diets of all six taxa examined. This copepod species has not been noted in other studies as being such an important dietary component and the reason for

its importance at San Onofre is unknown. *Euterpina acutifrons* may be more abundant near San Onofre than elsewhere (mean density 10,640/m^3—range 1,078–37,314/m^3—between the 9 and 100 m isobaths during a microzooplankton study conducted at San Onofre during the year prior to the feeding study), or it might have been unusually abundant during the year when the feeding studies were done, but appropriate data from long-term and larger scale studies that would allow evaluation of these suggestions are unavailable. Other particularly important copepods were the cyclopoid *Oithona oculata* and the calanoid *Labidocera trispinosa*. However, copepods were not the only important food items in the nearshore zone and were not the dominant prey for some of the Pr stage larvae. Other consistently important prey included tintinnids, especially *Stenosomella* spp., and mollusc veligers (principally bivalves, but also gastropods in some cases). Older sciaenid larvae consumed appreciable numbers of mysids. The diets of the older larvae did not exclude small items such as mollusc veligers or copepod nauplii; instead, the small items continued to be consumed, and larger items such as larger copepod species (e.g., Barnett and Jahn 1987: table 3) were added as well. This is consistent with Hunter's (1981) observation that although the maximum prey size selected increases more or less rapidly with increasing larval fish size, the minimum prey size increases very slowly. Thus larger larvae can select from among a wider range of prey sizes, consuming the energetically more valuable larger items when those are available, and perhaps maintaining on smaller items when large prey are unavailable (Hunter 1976; Hunter and Kimbrell 1980).

Concurrent plankton sampling that would allow comparisons of the spatial distributions of the fish larvae and their prey species was not part of the present study. However, other studies did examine the distribution and abundance of the zooplankton during the day in the same area from 1977 through 1980 (Barnett and Jahn 1987), and spatial patterns of the fish larvae and their prey can be compared in a general way on the basis of these studies. The majority of the most important prey categories occurred in highest concentrations near shore (e.g., Barnett and Jahn 1987). For example, *Oithona oculata* was most abundant in the epibenthos shoreward of the 13 m isobath (Barnett and Jahn 1987), while *Paracalanus parvus* was abundant throughout the water column shoreward of the 30 m isobath (Fig. 1). The Marine Review Committee's unpublished count data, from samples collected at San Onofre on 31 October 1978 indicated that *Euterpina acutifrons* nauplii were approximately 4–34 times more abundant in samples taken at the 9, 13, and 30 m isobaths than in samples from the 100 m isobath (maximum abundance 141,200/m^3, averaged over the water column at 13 m), while the copepodites and adults were 1.5–19 times more abundant at the shallow stations than at the 100 m station (maximum abundance 11,600/m^3, averaged over the water column at 13 m). *Labidocera trispinosa* nauplii were restricted to the very nearshore zone, shoreward of the 13 m isobath, where they occurred throughout the water column (Fig. 1). Bivalve veligers were abundant throughout the water column between the 13 and 30 m isobaths, while gastropod veligers occurred throughout the nearshore zone and seaward to at least the 100 m isobath (Fig. 1). The most frequently occurring mysid taxa in the larval diets—*Holmesimysis costata*, *Neomysis rayii*, and *Neomysis* spp. juveniles—all were most abundant in the epibenthos shoreward of the 15 m isobath (Bernstein and Gleye 1981[4]). Clutter (1967) reported that *H. costata*, as well as several other mysid species, was restricted to the nearshore zone off La Jolla, CA.

Barnett et al. (1984) described the cross-shelf and vertical distributions of the larvae of five of the six fish taxa considered here. All five were most abundant shoreward of the 45 m isobath; larvae of the sixth taxon, *Paralabrax* spp., occur principally shoreward of the 36 m isobath (Lavenberg et al. 1986). The atherinid larvae are almost exclusively neustonic; *Paralichthys californicus* and the *Paralabrax* spp. larvae occur throughout the water column (especially in midwater); and the *Genyonemus lineatus* and *Seriphus politus* larvae are located mainly in the lower water column and epibenthos (Schlotterbeck and Connally 1982; Barnett et al. 1984; Jahn and Lavenberg 1986). Ontogenetic redistributions occur during the larval phase for at least some of the taxa: the flexion and postflexion stage larvae of *G. lineatus* and *S. politus* are more nearshore and epibenthic than the preflexion stage larvae (Barnett et al. 1984), while the transforming postflexion larvae of *Paralichthys californicus* occur most frequently and in

[4]Bernstein, B. B. and L. G. Gleye. 1981. The ecology of mysids in the San Onofre region. Volume II: New reports. Rep. Mar. Rev. Comm., Rep. No. MEC01281999.

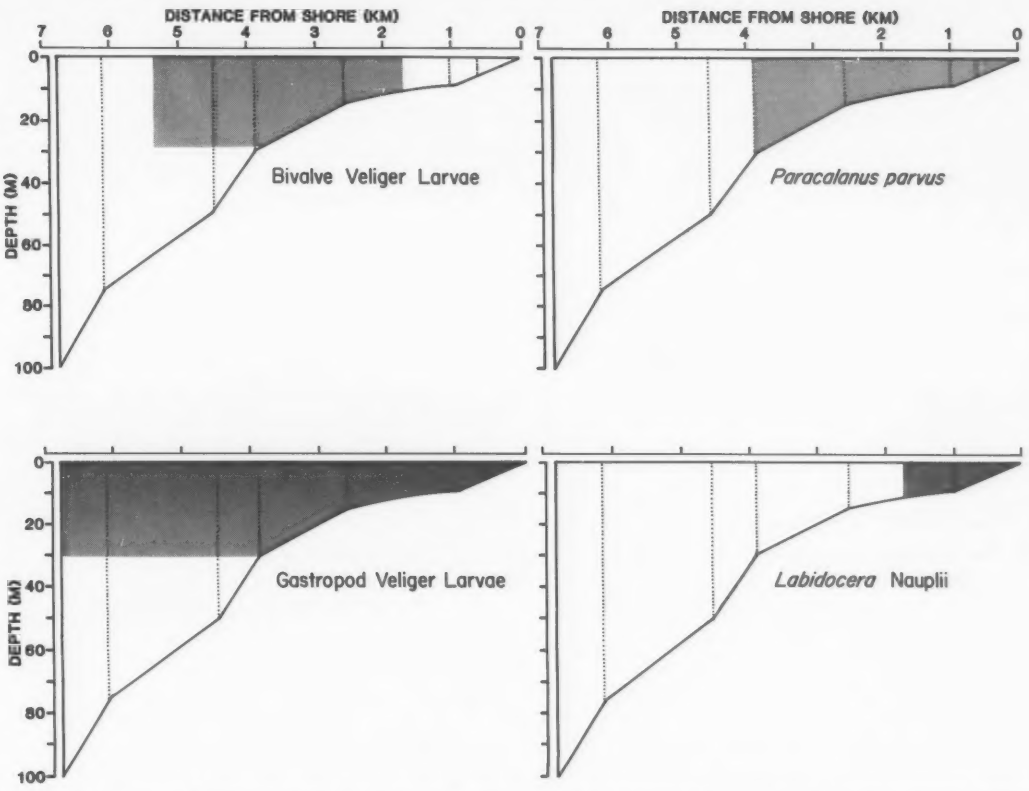
DISTANCE FROM SHORE (KM)
7 6 5 4 3 2 1 0
DEPTH (M)
0 20 40 60 80 100
Bivalve Veliger Larvae
DISTANCE FROM SHORE (KM)
7 6 5 4 2 1 0
Paracalanus parvus
DEPTH (M)
0 20 40 60 80 100
Gastropod Veliger Larvae
Labidocera Nauplii

FIGURE 1.—Zones of significantly higher concentration of four zooplankton taxa near SONGS. Shaded areas represent higher concentration as determined by nonparametric one-way ANOVA ($P < 0.05$) on number per m^3 data. Redrawn from Marine Review Committee Document 78-01, Annual report to the California Coastal Commission, September 1977–August 1978: Updated estimated effects of SONGS Unit 1 on marine organisms. August 1978.

highest abundance in the neuston shoreward of the 9 m isobath.

Thus the distributions of the fish larvae and their prey are broadly similar. However, the sharp vertical gradients in abundance patterns for the atherinids and the older sciaenid larvae apparently do not closely match the vertical patterns of their prey. In discussing the results of their respective larval fish feeding studies, both of which utilized concurrent larval fish and zooplankton sampling during the day and night, Brewer and Kleppel (1986) and Jahn et al. (1988) remarked on this lack of a close match between the vertical distributions of fish larvae and their prey in the shallow nearshore zone. They suggested that factors other than, or in addition to, feeding must be important in determining larval distributions in the nearshore zone. Avoidance of dispersal seaward, away from the shallow coastal zone, is likely to be one of the most important factors (e.g., Brewer and Kleppel 1986).

Nearshore currents off southern California are mainly parallel to shore, tend to reverse at roughly tidal frequency, and have only a weak cross-shelf component (e.g., Winant and Bratkovich 1981; Jackson 1986). A comparison of the variances of the longshore and cross-shelf current speeds off San Onofre (the variance of the current speed is a good measure of the energy of the coastal current) indicates that the variance of the longshore current (102 cm^2/s^2) is about four times that of the cross-shelf current (25 cm^2/s^2) (Elwany et al. in press). This stronger longshore current has a net southerly motion, while the weak cross-shelf current has a net shoreward motion (Marine Review Committee 1977[5]). Thus

[5]Marine Review Committee. 1977. Annual report to the California Coastal Commission, August 1976—August 1977, summary of the estimated effects on marine life of Unit 1,

plankters occupying the nearshore zone in the San Onofre vicinity will, on average, tend to be transported alongshore, but not out of the nearshore zone. Those plankters occupying the epibenthos, where currents are minimal, are especially likely to be retained in the nearshore zone (e.g., Barnett et al. 1984; Jahn and Lavenberg 1986; Barnett and Jahn 1987). At times, the nearshore plankton distributions at San Onofre are disrupted (Barnett and Jahn 1987), and during those times the neritic fish larvae may be transported seaward.

Tidal mixing and nutrient recycling in the nearshore zone allows high rates of phytoplankton production near shore (Petersen et al. 1986; Barnett and Jahn 1987). This production can be utilized directly by fish larvae (e.g., Lasker 1975, 1981), or indirectly in the form of microzooplankton and small macrozooplankton, both of which occur in high concentrations near shore (e.g., Lasker 1978; Barnett and Jahn 1987). The nearshore zone appears to provide a good feeding environment for fish larvae, on average. However, it appears that this resource is largely utilized only by the nearshore species, since the larvae of more offshore species are relatively rare in the shallow coastal waters (e.g., Gruber et al. 1982; Barnett et al. 1984). Lasker (1975) demonstrated that the food resources of the nearshore zone may be critical to the first-feeding larvae of the broadly distributed species *Engraulis mordax*, and Theilacker (1986) showed that first-feeding larval *Trachurus symmetricus*, a more offshore species, were less vulnerable to starvation in nearshore habitats around the islands off the California coast than they were in offshore waters. However, larval *T. symmetricus* are uncommon in shallow coastal waters and in general there is little evidence that the shallow coastal zone provides an important feeding resource for the larvae of offshore fish species.

The observations that the larvae of the offshore fish species apparently make little use of the food resources of the nearshore zone, and that among the larvae of the neritic species the distributions of the larvae and their prey do not closely correspond, suggest that food is not the primary influence in determining nearshore larval fish distributions. What the primary influence (or influences) is remains to be determined. It does seem reasonable to conclude, at least, that larval fish distributions within the nearshore zone are a function of the advantages conferred by remaining in this environment.

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Seasonal Differences in Spawning, Egg Size, and Early Development Time of the Hawaiian Anchovy or Nehu, *Encrasicholina purpurea*[1]

Thomas A. Clarke

ABSTRACT: Nehu spawning is concentrated in a 1 hour period shortly after sunset; the delay after sunset is longer in the winter than in summer. Incubation time for nehu eggs is 22–35 hours and is inversely related to temperature. Development time between hatching and first feeding shows relatively greater seasonal differences, and total embryonic development time during the coldest months is almost twice that of the warmest months. Nehu egg size is inversely related to temperature. The seasonal differences in egg size are probably the result of a physiological response to temperature. The potential adaptive value of the seasonal change in egg size in this tropical species is more likely related to size-specific differences in predation rates rather than to seasonal changes in abundance or size of food for larvae. The seasonal changes in total development time result in marked differences in the time of the diel cycle at which larvae reach first-feeding status; these differences could have more influence on survival of small larvae than effects related to either predation or food availability.

Seasonal differences in egg size, incubation, and posthatch embryonic development time have been reported for many species of temperate or higher latitude fishes. Some reports, e.g., Blaxter and Hempel (1963), involve differences between stocks or populations with different spawning seasons. Other examples, e.g., Ware (1977), deal with differences occurring over the spawning season of an apparent single stock. Hypotheses presented about the potential mechanisms or adaptive significance of seasonal differences are related to the rather marked seasonal changes in temperature, productivity, etc., that are typical of high latitude environments. Seasonal differences in egg size and early development have not been investigated in fishes from tropical latitudes where seasonal environmental changes are less extreme than at higher latitudes.

The Hawaiian anchovy or nehu, *Encrasicholina purpurea*, spawns throughout the year in enclosed, semiestuarine areas of Hawaii (Tester, 1955; Clarke 1987). Preliminary studies indicated that spawning occurs over a very short period after dusk. Because of this, it was possible not only to obtain freshly spawned eggs readily, but also to identify "day-classes" of eggs and prefeeding larvae throughout the diel cycle and thus to estimate incubation and development times from field samples. This paper reports on seasonal differences in spawning, egg size and development and considers hypotheses based on studies from higher latitudes in the context of seasonal environmental changes in the tropics.

MATERIALS AND METHODS

All material was collected from Kaneohe Bay, a semienclosed basin on the northeast side of the island of Oahu, HI. Plankton samples were collected with a 1 m diameter, 5 m long conical plankton net of 0.335 mm mesh. The net was rigged with a three-point bridle to which a ca. 3 kg weight was attached. The net was simply dropped mouth downward, allowed to fish to the bottom (12–15 m), and retrieved by a tether attached to a choke line about 1 m behind the mouth. The sample was immediatly preserved in a ca. 4% formaldehyde/seawater solution. The present study was conducted during the course of a long-term survey of nehu egg abundance that sampled stations throughout Kaneohe Bay between the hours of 0600 and 1100 at approximately weekly intervals. These samples provided eggs and larvae from the morning hours and also indicated periods and locations of high egg or larval abundance for sampling at other times of the day.

Previous studies (Clarke 1987) on adult female nehu indicated that spawning occurs during a short period (a few hours) after sunset. In order to determine spawning time more precisely, plankton samples were taken at hourly intervals between sunset and midnight at four different times of the year. Based on data from the most

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recent regular egg survey, one to three stations were sampled close to the solstices and equinoxes: 30 September 1984; 27 December 1984; 21 March 1985; and 26 June 1985. The hours sampled also included expected hatching time for the previous night's eggs for all dates except March, in which case samples were also taken at 0300–0430. The stations were also sampled in the afternoon, 1–2 days after the sunset to midnight series. Times of sunset and sunrise for the above dates were taken from astronomical tables. Water temperatures for each period were taken from the data log at the Hawaii Institute of Marine Biology laboratory at Coconut Island. Hourly surface temperatures for a 2 wk period bracketing the sampling were averaged.

Nehu eggs and larvae are easily identified. Eggs were usually very numerous (100's per sample) and were either all at very nearly the same stage or, for certain times of the day in December and March, readily separated into two age groups: eggs from the most recent spawning and much more developed eggs from the previous night's spawning. There were many fewer larvae in the samples (typically 10's per sample); in several cases larvae from 2 to 4 different samples taken within an hour of each other were combined in order to assess development at a given time of day. Larvae less than 4 mm notochord length could be separated into either two or three age groups based primarily upon presence or absence of yolk, pectoral fins and rays, and eye pigmentation. Between appearance of the pectoral fin buds and development of pectoral rays, age groups could be further discriminated using the diameter of the roughly semicircular pectoral fin bases relative to that of the pupil or the orbit (neither of which appeared to increase significantly after the pectoral buds appear). Other characters such as the development of the mouth or the gut were correlated with the principal characters used, but were not as useful for qualitative separation. For any given time of day, the least developed larvae were considered "0" group larvae (0–24 h past hatching); the next most developed, "1" group (24–48 h past hatching); and the third, if present, "2" group (48–72 h past hatching).

Except for the late afternoon samples from June, there was no difficulty in separating small larvae into age/development groups, i.e., larvae in each of the two or three groups present were similar to each other and there were no intermediates. In the June series, the apparent oldest group of afternoon larvae showed a broader range of several features than was evident for similar stages at other seasons. There was, however, still no overlap with younger stages, and after examination of more larvae from other afternoon samples taken at the same time of the year in 1984 and 1985, it was concluded that these larvae represented only one variably developed age group (see Results section). Larvae larger than 4 mm notochord length were taken infrequently, and it was not possible to estimate age groups among these on the basis of either size of development.

Volumes and dry weights were determined for undamaged newly spawned eggs from each season. Nehu eggs are ellipsoidal with the major axis about twice the minor. The yolk mass is similarly shaped and separated from the chorion by an obvious pervitelline space. For 40–50 freshly spawned eggs from each season (except June when only 29 eggs with no visible embryo were available), the major and minor diameters of both the entire egg and the yolk within were measured to the nearest 0.01 mm using an ocular micrometer at 100× magnification. Egg and yolk volumes were calculated using the formula for a prolate spheroid. Replicate samples (3 per season) of 20 eggs each were rinsed with distilled water, placed in a preweighed aluminum pan and dried at 60°C. Weights of empty and full pans were determined to the nearest 0.002 mg; weight per egg was calculated by subtraction and division by the number of eggs in the sample.

Dry weights were also determined for samples of 10–20 hydrated ovarian ova from spawning nehu taken by purse seine. Preliminary studies indicated that unless ova had already ovulated, they could not be reliably and completely separated from follicular tissue. The time between ovulation and spawning is apparently very short (Clarke 1987), and few samples of adult nehu contained many fish in this condition. Consequently, the only data reported here were from 10 females taken from a purse seine collection on 1 June 1983. This collection contained the widest size range (39–61 mm SL) of females with ova free in the oviducts.

Notochord lengths of larvae were measured to the nearest 0.1 mm. There were, however, usually less than 10 larvae of each day class at each different time of day, and statistical comparisons of average length between seasons for the same stages were not possible. The numbers of undamaged larvae suitable for dry weight determinations were even lower. Dry weight determinations were made for only three samples

of 5–10 larvae each from September and six samples of 10 each from March.

RESULTS

Spawning

The dusk-to-midnight samples from all four seasons clearly indicated that spawning was concentrated within a ca. 1 h period shortly after sunset. Newly spawned eggs, with no evidence of embryonic development under low magnification, were absent from initial samples and appeared in large numbers in samples 1.5–3 hours after sunset. The eggs in samples taken ca. 1 hour after first appearance of new eggs were already either mostly or totally in early cleavage stages. In the June series, many of the new eggs in the first sample containing new eggs were already in early cleaveage stages. Newly spawned eggs were very rare in samples taken ca. 1 hour after first appearance and were absent from later samples. Thus spawning appears to be concentrated within a period of 1 hour or less. The estimated midpoints of spawning time (Table 1) indicate that spawning occurs about 3 hours earlier in winter than in summer. The difference is not entirely accounted for by the earlier sunset in the winter months; the delay after sunset is less than in summer. These estimates of seasonal changes in spawning time agree with trends evident from mature females (Clarke 1987).

Incubation

In June and September, the incubation period was less than a day, and two day classes of eggs never occurred in the same sample. By early morning, embryos already extended about halfway around the remaining yolk. By late afternoon they extended over three-fourths of the way around the yolk, and the tail had flexed sideways. In both months the eggs apparently hatched about 22 hours after spawning time. During a 1 h period the "old " eggs disappeared, and newly hatched larvae appeared.

Incubation time was considerably longer in December and March. Eggs taken in the morning and afternoon were noticeably less developed than those from the same times in June or September. Both "old" eggs and recently spawned eggs were present between spawning time and midnight in December. No "old" eggs were present in any morning samples, and the embryos in the latest (2400 h) night samples appeared almost ready to hatch, judged from comparable stages in the June and September samples. Thus

TABLE 1.—Summary of data on spawning time, duration of egg and prefeeding larval stages, and egg size of the Hawaiian anchovy, *Encrasicholina purpurea*, in September and December 1984 and March and June 1985. Times of sunrise, sunset, spawning, and hatching are Hawaiian Standard Time. Temperature values are the means and ranges of hourly surface temperatures for a 2 wk period bracketing the sampling dates (see text). Values for egg and yolk volume are means and standard deviations of volumes calculated from length and width measurements.

	Sept.	Dec.	Mar.	June
Sunset	1800	1730	1800	1900
Sunrise	0600	0645	0600	0515
Spawning	2100	1900	2000	2200
Hatching	1900	0100	0700	2000
Temp. (°C) (range)	27.7 (27.4-28.1)	23.1 (22.5-23.9)	22.2 (21.6-23.1)	26.5 (25.9-27.1)
Incubation (h)	22	30	35	22
Hatch-feeding (h)	35	54	71	47-57
Total (h)	57	84	106	69-79
Egg weight (g)	14.8	17.9	19.5	14.9
Egg vol. (mm^3) (SD)	0.195 (0.023)	0.248 (0.024)	0.262 (0.019)	0.211 (0.016)
Yolk vol. (mm^3) (SD)	0.168 (0.020)	0.204 (0.025)	0.222 (0.022)	0.166 (0.017)

hatching time was probably about 0100 and total incubation time about 30 hours. In March, old eggs were present along with new eggs between spawning time and 0430, but were absent from the earliest postsunrise sample taken at 0820. Old eggs were, however, present in samples taken at 0600–0700 earlier in March; this indicates that hatching time was probably about 0700 and that incubation time was about 35 hours.

Early Development

Development to first feeding status was most rapid in September (Table 2). By the end of the first day, the yolk sac had disappeared, and the pectoral fin bases were almost the same diameter as the eye. By the morning of the second day, the "1" larvae had black eyes and pectoral fins with well-developed rays; most individuals had food items in the gut. Similar larvae occurred in samples taken nearer to sunrise on other dates in September–October. Thus it is likely that the "1" larvae were ready to feed at or near sunrise and that development time from hatching to first feeding was about 35 hours (Table 1).

Development was considerably slower in December and March (Table 2). Some yolk remained at the end of the first day in both months. In December, "2" larvae had already been feeding by 0800 and probably reached feeding status at or near sunrise or about 54 hours after hatching. In March, early "3" larvae taken at 0845 had already been feeding, and the late "2" larvae appeared to have reached feeding status at or just before sunrise, about 71 hours after hatching.

In June the larvae developed almost as fast during the first day as in September (Table 2), but little change took place over the second night. In the morning only a few of the "1" larvae had traces of eye pigment. By afternoon there was a relatively wide range of development among apparent "1" larvae; they had white to brown eyes and variably developed pectoral rays. The mouths of some individuals appeared

TABLE 2.—Developmental characters of different age groups of early larvae of the Hawaiian anchovy, *Encrasicholina purpurea*, at different times of the day for four different sampling dates. Codes for yolk sac (Y) are: + = present along ventral margin, T = traces anteriorly, 0 = absent; for pectoral fin; 0 = absent, B = buds visible, P = diameter of bases about equal to that of eye pupil, E = bases diameter about equal to that of eye, and R = fin rays visible; for eye pigment (E): 0 = none, T = trace, Br = brownish, Bl = black, fully pigmented. Very early stages, which would otherwise be coded "+-0-0", are coded as "NH" or "STR" depending upon whether the larvae were newly hatched and still bent anteriorly or had straightened, respectively. Larvae apparently developed to feeding status, which would otherwise be coded "O-R-Bl", are simply designated by "F".

Date / Time	Age group: Character:	"0" Y–P–E	"1" Y–P–E	"2" Y–P–E
September 1984				
1900		NH	O-E-O	
2200-2300		STR	O-E-T	
1030		T-B-O	F	
1600		O-P-O	F	
December 1984				
0800		NH	T-P-O	F
1830		STR	O-E-O	F
2330		T-O-O	O-E-T	F
March 1985				
0830		NH	T-B-O	O-E-T
1500		STR	O-P-O	O-E-?
2030-2330		+–O–W	O–E–O	O–E–Br/Bl
0330–0430		+–B–O	O–E–T	O–R–Bl
June 1985				
2100–2200		NH	O–B–O	F
0800–0900		T–B–O	O–E–O/T	F
1400–1800		O–P–O	O–R–O/Br	F

nearly fully developed. In the night samples, all early "2" larvae appeared developed to feeding stage and some had traces of food in the gut; "2" larvae in morning samples were feeding. Thus some of the June larvae may have reached feeding status just before sunset or ca. 47 hours since hatching, but many apparently did not develop to this point until after dark and did not start feeding until the next morning or about 57 hours since hatching (Table 1).

Egg Size

Dry weight and volume estimates indicated that egg size was about the same in September and June, but ca. 25% and 30% larger in December and March, respectively (Table 1). The ratios (Sept.:Dec.:Mar.:June) of estimated dry weight per egg were 1:1:21:1.32:1.01. Similar ratios for average yolk volume (1:1.21:1.32:0.99) were closer to those for weights than were the ratios for whole egg volume (1:1.27:1.34:1.08). Yolk volume averaged 79–86% of whole egg volume with no evidence of a trend with egg size. The ratios of egg to yolk for both width and length ranged between 1.05 and 1.09. Except for a value of 2.07 for March yolk length to width ratio, the other length to width ratios for both egg and yolk ranged from 2.16 to 2.26.

Available data on larval size are few, but indicate a positive relationship with egg size. In all months, the newly hatched larvae were about the same length (2.0–2.2 mm), but larvae at or near first feeding status were 3.0–3.7 mm long in March and December as opposed to 2.8–3.0 mm in September and 3.0–3.5 mm in June. Mean dry weights of late "0" and early "1" larvae from September and March were 63% and 65%, respectively, of mean egg weights for the same periods, indicating commensurately heavier larvae from the larger March eggs.

The average weight per egg of hydrated ova taken from 10 females 39–61 mm standard length was 17.8 μg. The estimates from different individuals ranged between 14.4 and 19.2 μg/egg. The value for the smallest female was well below that of the other nine (42.5–61 mm SL); the next lowest value was 16.3 μg/egg. There was, however, no correlation between average weight per egg and female length for the whole series ($P > 0.20$, Spearman rank correlation coefficient).

Discussion

The observed seasonal differences in nehu reproductive parameters are not likely owing to genetic differences between seasonal subpopulations. Nehu reach spawning size at an age of 3–4 months and rarely live as long as six months (Struhsaker and Uchiyama 1976). Thus the progeny of, e.g., March spawners would be spawning in July–September rather than the following March. Although annual changes in environmental factors in Hawaii are fewer than at higher latitudes, nehu spawn throughout the entire year rather than over a short season, and the observed differences in spawning time, egg size, etc., are most likely responses to changes in temperature, day length, light levels, etc., encountered over the entire annual cycle.

The movement of adult nehu to spawning areas and their near synchronous release of eggs are probably stimulated by decreasing light levels in the afternoon and evening, but the timing is not simply related to seasonal changes in day length and time of sunset. The delay between sunset and spawning was less in the winter, possibly because light levels in the water column decrease earlier, relative to sunset, in the winter than in the summer owing to differences in solar elevation. It is also possible that responses to light are modified by some other seasonal factor, e.g., temperature.

Seasonal changes in egg size have been reported from apparently the same stock for many other species of fishes. For example, Ware's (1977) data on egg diameters of *Scomber scombrus* in the Gulf of St. Lawrence indicate that egg volume at the beginning of the spawning season (early June) is about twice that at the end (mid-August). The central population of the northern anchovy, *Engraulis mordax*, is more similar to nehu in that it spawns year round, and maximum egg volume, which occurs in March, is about 20% greater than the minimum in September–October (Hunter and Leong 1981).

Several mechanisms for within-stock, seasonal changes in egg size have been suggested. Egg size may be related to size of the spawning females, and the seasonal trend in egg size due to the larger females' spawning early in the season and the smaller ones later (Bagenal 1971). The data on ovarian egg weights from spawning nehu indicate no relation between egg size and female size; furthermore, there is no evidence of seasonal changes in size composition of spawning nehu. Clarke (1987) found no difference in size composition between winter and summer spawners examined for fecundity; unpublished data from that study show that size composition of

spawning nehu fluctuates throughout the year, but that there is no tendency for e.g., March spawners to be larger (or smaller) than September spawners. Egg size has been shown to be both positively and negatively affected by food supply or ration (Bagenal 1969; Hislop et al. 1978). The abundance of macrozooplankton, upon which adult nehu feed, does not appear to change systematically with season in Kaneohe Bay (Hirota and Szyper 1976). Daily ration or the fraction available for reproduction could, however, change seasonally due to differences in temperature or day length, but relevant studies to consider this possibility have not been done.

Imai and Tanaka (1987) demonstrated that egg size of *Engraulis japonica* responds more directly to temperature changes, and several potential mechanisms have been proposed. Daoulas and Economou (1986) suggested that egg size would be inversely correlated with temperature if oocyte differentiation rates increased relative to oocyte growth rates with increasing temperature. Tanasichuk and Ware (1987) hypothesized that gonadotropin secretion rates increase with temperature and cause a decrease in preovulatory atresia. For a given effort per batch, this would result in more, but smaller eggs at ovulation. Nehu fecundity is higher in the summer when egg size is lowest, and the increase in the summer is only partly accounted for by higher effort per batch (Clarke 1987). If effort per batch is controlled by some other factor, either of the above hypotheses could apply to nehu.

Several studies have hypothesized that both within- and between-stock differences in egg size are adaptive and related to minimizing mortality owing to starvation of early larvae. Blaxter and Hempel (1963) showed that larvae from large herring eggs were probably better able to survive situations with low food abundance. Ware (1977) showed that egg size in *Scomber scombrus* was positively correlated with the size of food items available for newly hatched larvae. There is, however, no evidence that nehu larvae encounter marked seasonal changes in food abundance or size. Kaneohe Bay is highly productive all year; Hirota and Szyper (1976) found no seasonal trends in total microzooplankton abundance. My own unpublished data indicate that concentrations and sizes of small copepod nauplii, the dominant prey of first-feeding nehu larvae (Burdick 1969), are similar throughout the year.

Ware (1975) and Tanasichuk and Ware (1987) have shown that a mechanism resulting in a decrease in egg size with increasing temperature would be selectively advantageous if egg and larval mortality rates were inversely related to egg size and if incubation times were inversely related to temperature (and not to egg size). Small nehu eggs and larvae would probably be subject to higher mortality owing to predation than would larger eggs and larvae at all times of the year, regardless of the apparent lack of variability in larval food supply. Furthermore, Yamashita's (1951) results indicate that differences in incubation time are caused by temperature and not egg size. Yamashita incubated nehu eggs from a single sample from Kaneohe Bay at different temperatures. Allowing for the fact that all his eggs had already spent a few hours at ambient temperature, the change in incubation time with temperature was similar to that evident from the seasonal data of the present study. Similar studies on other engraulids (King et al. 1978; Lasker 1964) have also shown negative correlations between incubation time and temperature that were presumably independent of egg size. Thus Ware's (1975) basic assumptions and hypothesis about factors selecting for egg size-temperature relationships seem to be applicable to nehu.

The duration of the period between hatching and first feeding (HF) was also negatively correlated with temperature. There were, however, seasonal differences in the ratio of posthatch to prehatch embryonic development time. HF was 1.60, 1.78, 2.02, and 2.14 times incubation time for September, December, March, and June, respectively (using HF = 47 hours for June). This indicates either that the effects of temperature on HF are qualitatively different from those on incubation, or that some other factor also affects posthatch development rate. For a range of temperatures that included those observed in this study, Houde (1974) showed that increasing temperature caused decreases in the period between hatching and eye pigmentation of larval *Anchoa mitchelli*. To the extent that seasonal differences in HF of nehu are similarly caused by temperature differences, this would tend to augment any selective advantage for larger eggs and larvae during the winter.

Even though Ware's (1975) hypothesis could potentially apply to nehu, the point in the diel cycle at which larval feeding becomes possible could have more important consequences to larval survival than differences in either egg size or

total development time. Small nehu larvae feed only during the day (Burdick 1969; Johnson 1982). In September, December, and March, larvae reached first-feeding status at or shortly before sunrise, could begin feeding as soon as they were able, and had an entire day to feed before having to survive the next night. In June, however, the larvae reached first-feeding status near sunset, had little or no chance to feed, and had to survive the night mostly or solely on internal reserves. Nehu larvae would face situations similar to June whenever the total time from spawning to first-feeding status was close to a multiple of 24 hours. (Other such periods would have occurred between September and December, between December and March, and between March and June.) If larvae during such periods had exhausted their internal reserves before they had a chance to feed, survivorship could have been greatly reduced compared with periods when larvae reached first-feeding status near dawn.

The time between reaching first-feeding status and irreversible starvation of nehu larvae is not known. It is usually of the order of days for fishes from higher latitudes (Hunter 1981), but is probably considerably less for nehu given that their incubation and development times are much shorter than those of most higher latitude species. Houde (1974) found that survival and growth of larvae of *Anchoa mitchelli* at 22°–28°C was unaffected by delaying feeding up to 24 hours or more after development of eye pigmentation, but nehu may be less tolerant. The development time between hatching and feeding status is longer for nehu than for *A. mitchelli* at similar temperatures, and visible yolk is gone at an earlier stage in nehu.

The seasonal changes in total time between spawning and reaching first-feeding status thus could result in fluctuations of mortality rates of nehu larvae throughout the year independent of either food supply or predation rates. Such fluctuations would not be expected in species from higher latitudes because differences of a few hours between reaching first-feeding status and the opportunity to feed are probably not as critical. Furthermore, spawning in many species, e.g., the northern anchovy, *Engraulis mordax*, is not as synchronous as in nehu and is spread over a broader portion of the diel cycle (Hunter and Macewicz 1980). Consequently, larvae from a given day's cohort would reach first-feeding status at various points during the diel cycle regardless of the absolute duration of the period between spawning and HF status.

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Larval Production and Mortality of Pacific Saury, *Cololabis saira*, in the Northwestern Pacific Ocean[1]

Yoshiro Watanabe and Nancy C. H. Lo

ABSTRACT: Because quantitative samples of saury eggs are difficult to obtain owing to their adhesive nature, reproductive level of the Pacific saury, *Cololabis saira*, has been estimated from the standing stock of the larvae and juveniles in Japan. Mortality curves were constructed and daily larval production at hatching was estimated for combined data from 1972 to 1986 and for consecutive individual years within this period. Durations of size classes were estimated from a growth curve and used to calculate fish production at age. Because number of fish captured by a net tow (area = 401.3 m^2) showed a diel cycle due to fish behaviors, such as net frame evasion and diel vertical movement, the average mortality curve for 15 years was based on data collected at night. We used an exponential decay model to describe the mortality of saury larvae and juveniles. The daily instantaneous mortality rate was 0.078, and the larval production at hatching was 1.255 larva/tow/day. Mortality curves for the individual years were based on data collected throughout the day and night after correction by size- and time-specific retention rates. Daily larval production at hatching fluctuated among individual years ranging from 0.154 to 5.176. Daily instantaneous mortality rates positively correlated with larval production at hatching, which might indicate the presence of a density-dependent process in larval mortality.

Together with the Japanese sardine, *Sardinops melanosticta*, and the mackerels, *Scomber japonicus* and *S. australasicus*, the Pacific saury, *Cololabis saira* (Brevoort), is one of the most important offshore pelagic fishes in Japan. Although total catch of the saury in Japan (210,000 t [metric tons] in 1984) was much smaller than that of the sardine (4,180,000 t) or the mackerels (810,000 t) (Statistics and Information Department, Japan 1986), more than 95% of the catch is destined for human consumption (Japan Saury Fishery Association 1985). In sharp contrast, the sardine (81%) and the mackerel (40%) catches (Fisheries Agency 1985) are procesed for animal foods.

Saury fishermen in Japan expect to have a reliable fishing forecast provided by the Tohoku Regional Fisheries Research Laboratory, Fisheries Agency of Japan, every summer before the beginning of the fishing season. The forecast includes the expected catch in the coming season and the potential fishing grounds. The expected catch depends on fish stock size, and the location and size of the fishing grounds are a function of fish migration in relation to oceanographic conditions. Fish stock size is determined by both reproductive level and mortality rates of developmental stages from postspawning through recruitment. Since the saury grows rapidly and becomes an adult within one year (Watanabe et al. 1988), larval production and mortality rate in young stages are believed to be more or less directly related to recruitment and catchable stock size. Matsumiya and Tanaka (1978) suggested from their intensive study of population dynamics of the northwestern Pacific saury that the fluctuations of population size are seriously affected by reproductive success.

An egg survey may be the best method for estimating the reproduction level of pelagic fishes. However, it is difficult to conduct a quantitative egg survey of the saury by towing plankton nets because the eggs attach by filaments to floating objects such as drifting kelp. We therefore have been conducting larval and juvenile surveys to estimate the reproductive level. We use catch/tow (number of fish/net tow) values of several size classes as abundance indices. The year-to-year changes of the indices may reflect the fluctuation of reproductive level.

The apparent number of larvae in a size class is influenced by the duration of growth through that size class. If growth is slow, the duration will be extended; conversely, if growth is fast, the duration will be short. The duration of growth through a size class thus defines the

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amount of time that larvae or juveniles are vulnerable to capture. Because the growth rate is not constant over the size range of the young fish sampled in this study, we must correct for this bias. The production of larvae by age is defined as the abundance of larvae by size divided by the duration of growth through the size class, which is expressed as catch/tow/day. This allows us to calculate instantaneous mortality rate (IMR), and thus, construct a mortality curve. We need to know age and growth rate of saury to calculate production at age and mortality rates.

In northern anchovy, *Engraulis mordax*, there have been extensive studies of eggs and larvae, and the methods to calculate the production and mortality rate were established (Zweifel and Smith 1981; Lasker 1985; Lo 1985; 1986). Ichthyoplankton survey data, embryonic incubation times, and larval growth rates are the essential parameters for this method. Further, one needs to have information on possible biases of tow data. For the Pacific saury, we have 15 years of larval net-tow data, a newly developed growth model based upon otolith growth increments (Watanabe et al. 1988), and information on bias correction of tow data for day and night differences. All these make it possible to compute fish production at different ages and mortalities. Extending the mortality curve to age 0, we can calculate larval production at hatching, which might be the best index of reproductive level so far available. In this paper we selected the exponential decay mortality curve and used it to calculate the larval production at hatching and the daily IMR of Pacific saury in the northwestern Pacific Ocean for 1972–86.

METHODS

Data Source

The Pacific saury spawns nearly all year round in the entire northwestern Pacific Ocean. The sampling areas and seasons were somewhat different from year-to-year, but our data set of 15 years (1972–86) included around-the-clock samples taken all year from a large area of the northwestern Pacific, lat. 29–45°N, long. 129–174°E (Fig. 1).

Saury larvae and juveniles were collected by a surface ring net that was towed for 5 minutes at 2 knots. The mouth diameter was 1.3 m, and therefore the surface area covered by one tow was 401.3 m^2. A mesh size of the 3.0 m forward part of the net was 2.0 mm, and the 1.5 m rear part was 0.33 mm. Samples were washed down after the 5 min tow and preserved in 10% unbuffered formalin. Larvae and juveniles of saury were measured to the nearest 0.1 mm knob length (KnL), the distance from the tip of the lower jaw to the posterior end of a muscular knob at the base of the caudal peduncle. They were then grouped into 11 size classes from 7.5 mm (including 5.0–9.9 mm) up to 57.5 mm (55.0–59.9 mm). The midpoint and both limits of each class were then converted into the capture size before preservation, using a shrinkage factor by formalin preservation (0.97) reported by Theilacker (1980) for northern anchovy. The midpoint of each size class was used to represent the class, though it is not a mean age of the class. The capture size was converted to age, and duration of each size class was obtained using the growth model developed by Watanabe et al. (1988). The growth equation from hatching to a 100 mm juvenile is

$$\mathrm{KnL} = 5.90 \exp((0.0865/0.0293) \times (1 - \exp(-0.0293\, t)))$$

where KnL is the fish knob length in mm after capture (before preservation) and t is the age in days from hatching.

Bias Corrections

An ichthyoplankton survey is essential for most pelagic fish research (Smith and Richardson 1977), but it is not bias free. The most common biases in catch of fish eggs and larvae are extrusion of eggs and larvae through net mesh and evasion of a net frame by fish. For the Pacific saury, the mesh size of the anterior part of the net, 2.0 mm, might be large enough to lose larvae by extrusion. Vulnerability of the fish to a net tow varies throughout a day due to changes in evasion abilities. Availability of the fish to a tow changes as well due to diel vertical movement. These factors result in differences in numbers of fish captured by net tows during the day and night. For the analysis, we defined 10 diel time periods based upon angles between the center of the sun and the celestial horizon. We used four periods in the morning—DAWN (DWN), MORNING TWILIGHT (MTW), SUNRISE (SRS), and MORNING (MRN)—and another four periods in the evening—AFTERNOON (AFT), SUNSET (SST), EVENING TWILIGHT (ETW), and DUSK (DSK). Time dura-

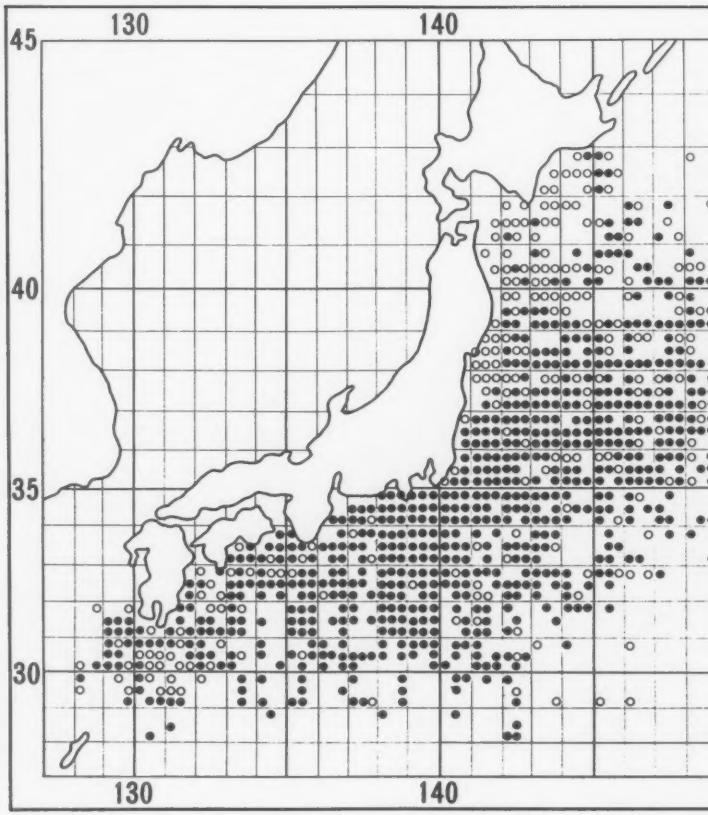
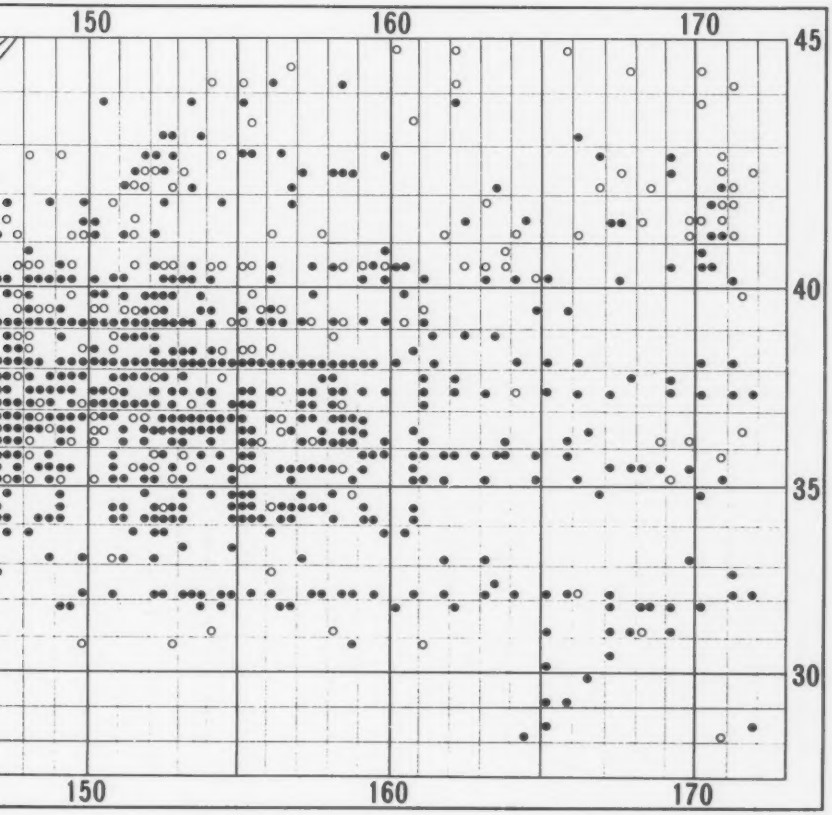


FIGURE 1.—Composite survey area of Pacific saury larvae and juvenil
where a positive tow has e



uveniles in the northwestern Pacific Ocean, 1972–86. Solid (open) circles represent areas
has ever (never) been recorded in the period.

tion between the end of MRN and the beginning of AFT was named DAYTIME (DAY), and the time duration between the end of DSK and the beginning of DWN was named NIGHTTIME (NIT). We examined the data collection of 15 years (1972–86) and estimated size- and time-specific retention rates. Changes of these values are due to the fish behaviors such as net frame evasion and vertical migration. The rates were calculated by taking ratios of catch/tow in each time category and that of the NIT (Table 1). Extrusion of larvae was examined as well, comparing observed numbers of fish with predicted numbers calculated from a mortality curve (see results section for detail).

To reduce the seasonal effect of larval production and mortality, we also considered the bias on average catch/tow within a year from unproportional sampling efforts among months. Net tows were concentrated between February and May; the percentage of juvenile fish in the total catch was low in winter and increased in spring and early summer (Fig. 2). Thus, we divided 12 months of the year into 4 seasons based upon the abundance of saury larvae and juveniles: January to March as the main spawning season, April to June as the late spawning season, July and August as the off spawning season, and Sep-

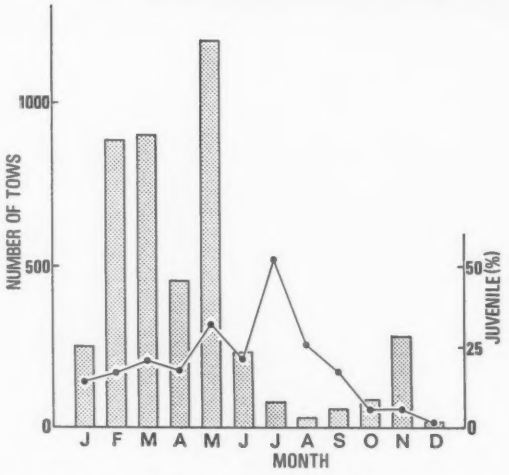


FIGURE 2.—Number of tows (columns) and percentage of juvenile Pacific sauries (dots) in total fish captured by months.

TABLE 1.—Annual average of Pacific saury catch/tow (c/t) and size- and time-specific correction factors (CF) of size classes in 10 time categories.

Size class (mm):		7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5
Time category (# tows)												
SRS	c/t	1.115	1.495	0.330	0.065	0.260	0.021	0.011	0.005	0.026	0.021	0.058
(92)	CF	0.864	0.724	0.220	0.072	0.475	0.064	0.050	0.029	0.215	0.158	0.450
MRN	c/t	1.588	2.281	0.521	0.352	0.154	0.043	0.039	0.028	0.019	0.003	0.000
(165)	CF	1.231	1.104	0.348	0.390	0.282	0.131	0.176	0.165	0.157	0.023	—
DAY	c/t	1.400	1.134	0.509	0.209	0.098	0.042	0.034	0.008	0.002	0.002	0.016
(1,517)	CF	1.085	0.549	0.343	0.232	0.179	0.128	0.154	0.047	0.017	0.015	0.124
AFT	c/t	2.090	2.004	1.022	0.403	0.176	0.039	0.018	0	0	0	0.003
(199)	CF	1.620	0.970	0.682	0.447	0.322	0.119	0.081	—	—	—	0.023
SST	c/t	1.486	1.175	0.937	0.501	0.524	0.189	0.006	0	0	0	0
(97)	CF	1.152	0.569	0.626	0.555	0.958	0.578	0.027	—	—	—	—
ETW	c/t	0.422	0.782	0.393	0.218	0.133	0.079	0.070	0.031	0.017	0.014	0.007
(132)	CF	0.327	0.379	0.262	0.242	0.243	0.242	0.317	0.182	0.140	0.105	0.054
DSK	c/t	1.425	1.700	1.354	0.867	0.641	0.268	0.340	0.428	0.192	0.121	0.084
(218)	CF	1.105	0.823	0.904	0.961	1.172	0.820	1.538	2.518	1.582	0.910	0.651
NIT	c/t	1.290	2.066	1.498	0.902	0.547	0.327	0.221	0.170	0.121	0.133	0.129
(1,805)	CF	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
DWN	c/t	0.803	1.465	1.285	0.750	0.499	0.313	0.205	0.152	0.082	0.088	0.053
(203)	CF	0.622	0.709	0.858	0.831	0.912	0.957	0.928	0.894	0.678	0.662	0.411
MTW	c/t	0.568	0.610	0.434	0.250	0.158	0.053	0.026	0.046	0.020	0.092	0.020
(80)	CF	0.440	0.295	0.290	0.277	0.289	0.162	0.118	0.271	0.165	0.692	0.155

[1]SRS = SUNRISE; MRN = MORNING; DAY = DAYTIME; AFT = AFTERNOON; SST = SUNSET; ETW = EVENING TWILIGHT; DSK = DUSK; NIT = NIGHTTIME; DWN = DAWN; MTW = MORNING TWILIGHT.

tember to December as the early spawning season (Fig. 3). We calculated catch/tow values of 4 seasons separately in every size- and time-group by summing up the number of fish and net tows of 15 years and then taking average catch/tow values of 4 seasons. These values, average catch/tow values of the year, were used for calculation of the size- and time-specific retention rates mentioned above.

Mortality Models and Computations

The mortality model of the young saury from hatching (age 0) to 52 days old (57.5 mm preserved KnL) was based on the data of catch/tow/day (daily production) at ages. Two types of mortality curves were fitted to both the combined data collected in the NIT period for 1972–86 and the data set from 14 individual spawning years. One mortality curve is based on an age-dependent instantaneous mortality rate (IMR), $Z_1(t) = \beta/t$, and the other based on the age-independent constant IMR, $Z_2(t) = \alpha$, where t is the fish age in days and α and β are coefficients of IMR. The age-dependent IMR was considered because of the possibility that early larvae may suffer higher mortality than the older ones, as in the case of northern anchovy larvae along the California coast (Lo 1985, 1986). We constructed both mortality curves for saury larvae and juve-

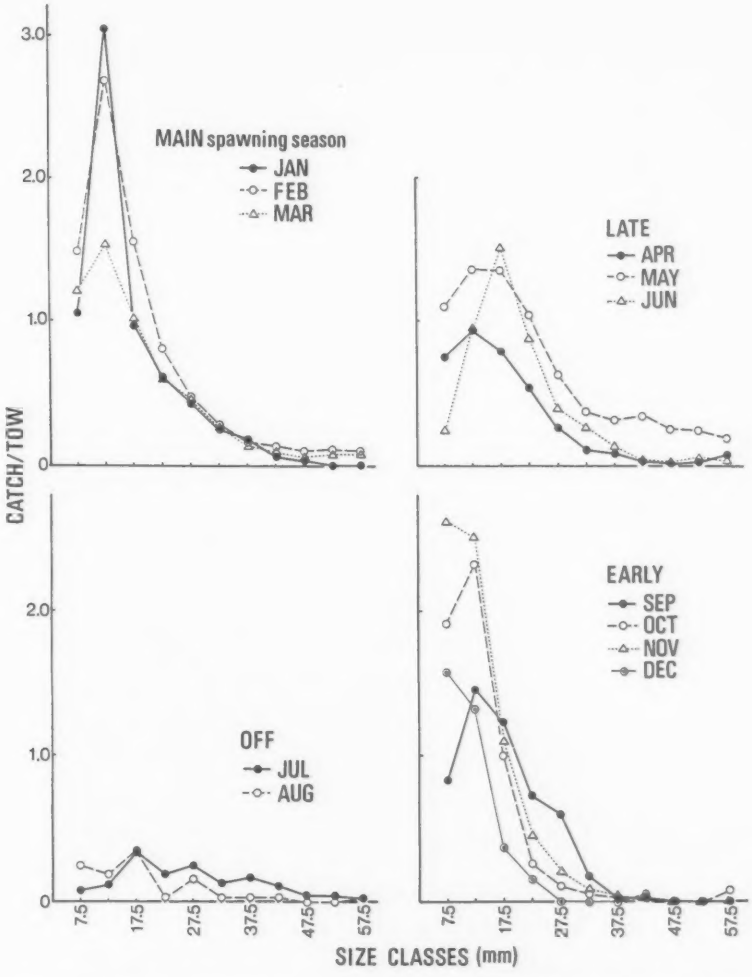


FIGURE 3.—Division of the year into four spawning seasons based on the number of Pacific sauries captured by a net tow (catch/tow) by months.

niles. The mortality curves based on $Z_2(t)$ fitted the larval and juvenile data better than $Z_1(t)$, and therefore, we chose $Z_2(t)$ to describe the fate of young sauries. The mortality curve with a constant IMR takes the form of the exponential mortality curve,

$$P_t = P_0 \exp(-\alpha t)$$

where P_t is the daily fish production at age t, t is the age in days from hatching, P_0 is the daily larval production at hatching, and α is the daily IMR.

For the computation of larval production and mortality rate averages of 15 years, we used the data of the NIT category. For the computations of individual years, however, the number of NIT samples were not sufficient; therefore, we had to use the data from all the time periods. The data sets of individual years were classified into 10 time periods of 11 size classes and were corrected by dividing numbers of fish by their specific retention rates (Table 1). The corrected numbers of fish were summed up in each size class and divided by the total number of tows of the year to calculate catch/tow values as the abundance index of each size class.

We used the catch data of the early, main, late, and off spawning seasons (from September to August of the following year) as a unit of a spawning year instead of the calendar year. According to the recent growth model by Watanabe et al. (1988), the saury becomes adult within a year, so, we supposed that the larvae produced in a spawning year constitute the major part of the year class of the current year.

The catch/tow value of each size class was further divided by the duration of the corresponding size class. This provided the production rate (catch/tow/day), which was used for the computation of larval production at hatching and mortality. The parameters, larval production at hatching (P_0) and daily IMR, are estimated by using a nonlinear program (Par (Dixon et al. 1985)).

RESULTS

The Overall Mortality Curve for 1972–86

To understand the fate of young sauries from 1972 to 1986, the average catch/tow/day from the NIT samples (Table 2) was used to estimate the larval production at hatching and the IMR. All the fish were first grouped into 11 size classes, ranging from 7.5 mm (5.0–9.9 mm) to 57.5 mm (55.0–59.9 mm), and the midpoint of each size classes was converted to age. The data from the first two size classes (7.5 mm and 12.5 mm) were excluded from the analysis because the catch/tow/day in these two size classes was lower than the next older larvae. The downward bias could be due to extrusion of the larvae through the mesh. The estimates of the larval production at hatching (P_0) and daily IMR were 1.255 larvae/tow/day (SE = 0.111) and 0.078 (SE = 0.004), respectively (Fig. 4). The total daily mortality rate ($(P_{t-1} - P_t)/P_{t-1} = 1 - (\exp(-\alpha))$) was 7.5% from the newly hatched larvae to the 52 d old juvenile.

TABLE 2.—Daily production (catch/tow/day) at age (day) of Pacific saury from NIGHTTIME samples, 1972–86.

Midpoint size (mm)	pr[1]	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5
	cp[2]	7.7	12.9	18.0	23.2	28.4	33.5	38.7	43.8	49.0	54.1	59.3
Age (day)		3.2	10.5	16.2	21.3	25.9	30.3	34.5	38.8	43.1	47.4	52.0
Size range (mm)	pr	5.0–	10.0–	15.0–	20.0–	25.0–	30.0–	35.0–	40.0–	45.0–	50.0–	55.0–
	cp	5.2–	10.3–	15.5–	20.6–	25.8–	30.9–	36.1–	41.2–	46.4–	51.5–	56.7–61.8
Stage duration (day)		7.1	6.4	5.3	4.9	4.4	4.3	4.2	4.3	4.3	4.4	4.7
# fish observed		2,030	3,982	3,352	2,148	1,333	821	536	406	330	375	351
Catch/tow		1.125	2.206	1.857	1.190	0.739	0.455	0.297	0.225	0.183	0.208	0.194
Daily fish production		[3]0.158	[3]0.345	0.350	0.243	0.168	0.106	0.071	0.052	0.043	0.047	0.041

[1]Fish knob length after preservation.
[2]Fish knob length after capture (before preservation).
[3]Not used for the computation.

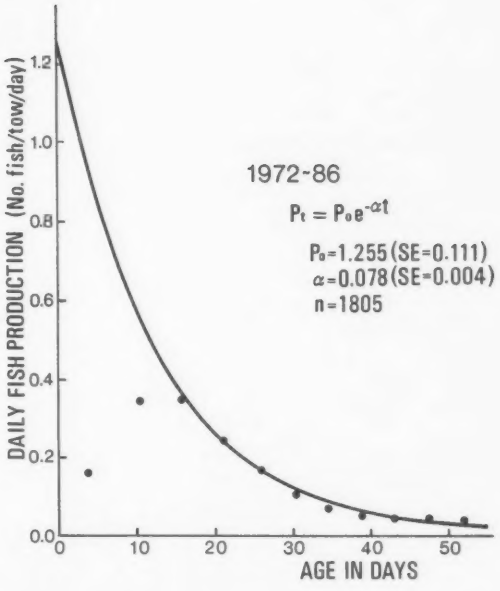


FIGURE 4.—Mortality curve of young Pacific saury calculated from fish production at ages calculated from the NIT data of 15 years (1972–86). Data points of the smallest two size classes were not used for the computation. P_0 is the larval production at hatching, α is the daily IMR, and n is the number of tow samples.

Mortality Curves for Individual Spawning Years

To assess the mortality of young saury for individual spawning years, we used all the tow data collected around the clock, after the correction of catch data by the size- and time-specific retention rates (Table 1). The correction procedures are the same for all the spawning years. To illustrate the data assemblage and computation, the 1979 catch data set for 11 size classes was given (Table 3). Again, the data points of the first two size classes were not used in the estimation procedure because of the apparent downward bias. The parameter estimates and the mortality curves are summarized in Table 4, and the mortality curves are presented in Figure 5.

The larval production at hatching (P_0) fluctuated by more than 30-fold from the maximum 5.176 larvae/tow/day in 1978 to the minimum 0.154 in 1985 spawning year. Daily IMR has also ranged from 0.115 down to 0.041, with daily mortality rates of 10.9% and 4.0%, respectively.

Year-to-year fluctuations of these two parameters (P_0 and IMR) and the total catch of saury in Japan (Statistics and Information Department, Japan 1987) are presented in Figure 6. The total catch of saury can be an index of the stock size, though possibly including effects of economic factors such as fish price. The fishing season of saury opens in the first half of August and closes in the middle of December. Since the saury becomes adult in 9–10 months and 2 yr old fish were not found in the northwestern Pacific

TABLE 3.—Daily production (catch/tow/day) at age (day) of Pacific saury in 1979 spawning year (September 1978–August 1979).

Midpoint size (mm)	pr[1]	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5
	cp[2]	7.7	12.9	18.0	23.2	28.4	33.5	38.7	43.8	49.0	54.1	59.3
Age (day)		3.2	10.5	16.2	21.3	25.9	30.3	34.5	38.8	43.1	47.4	52.0
Size range (mm)	pr	5.0–	10.0–	15.0–	20.0–	25.0–	30.0–	35.0–	40.0–	45.0–	50.0–	55.0–
	cp	5.2–	10.3–	15.5–	20.6–	25.8–	30.9–	36.1–	41.2–	46.4–	51.5–	56.7–61.8
Stage duration (day)		7.1	6.4	5.3	4.9	4.4	4.3	4.2	4.3	4.3	4.4	4.7
# fish observed		607	1,267	738	420	194	68	61	32	16	13	9
# fish corrected		674	1,470	939	625	245	98	90	62	22	14	10
Catch/tow		1.685	3.676	2.349	1.562	0.613	0.244	0.226	0.155	0.054	0.036	0.026
Daily fish production		[3]0.236	[3]0.574	0.443	0.319	0.139	0.057	0.054	0.036	0.013	0.008	0.006

[1]Fish knob length after preservation.
[2]Fish knob length after capture (before preservation).
[3]Not used for the computation.

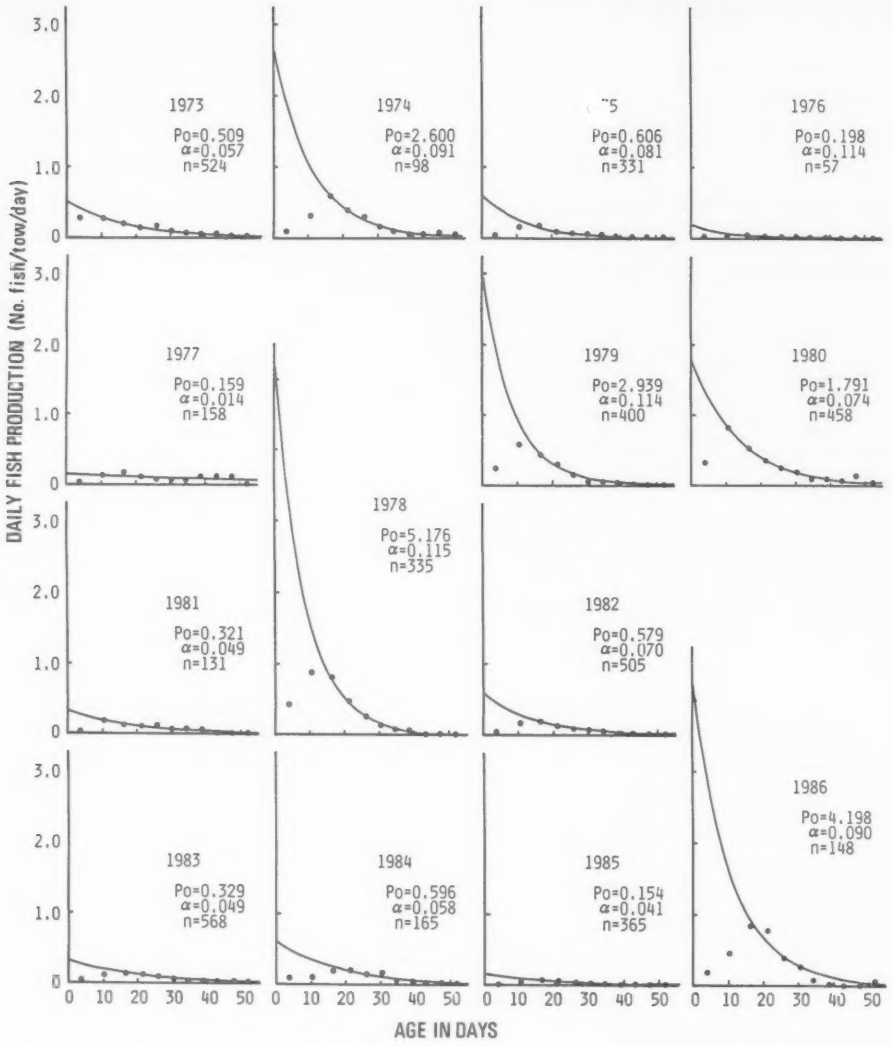


FIGURE 5.—Mortality curves of individual spawning years. P_0 is the Pacific saury larval production at hatching, α is the daily IMR, and n is the number of tow samples.

(Watanabe et al. 1988), the total catch in a fishing season must come from larvae produced in the spawning period of the same year. For example, the 1973 catch is related to larval production at hatching and daily IMR of the 1973 spawning year (from September 1972 to August 1973).

Larval production at hatching and the daily IMR have fluctuated somewhat concordantly from 1973 to 1986. The Spearman's Rho is 0.704 ($n = 14$, $P < 0.05$), indicating a positive correlation between P_0 and IMR among years. The exception to this trend was 1976. The production value of 1976 was one of the lowest in 14 years whereas the daily IMR was very high, probably resulting in a minimum catch of <100,000 t in 1976.

Mesh Retention of Larvae

The low values of larval production for the first two size classes precluded their use in the estimation of larval mortality. Since the mesh size of the anterior 3.0 m of the net is 2.0 mm, we

TABLE 4.—Daily larval production at hatching (P_0) and daily instantaneous mortality rates (IMR) of individual spawning years with standard error in parentheses.

Spawning year	P_0 (larva/tow/day)	IMR	Mean square error ($\times 10^{-4}$)
1973	0.509 (0.100)	0.057 (0.008)	4.05
1974	2.600 (0.410)	0.091 (0.007)	10.20
1975	0.606 (0.112)	0.081 (0.009)	1.37
1976	0.198 (0.080)	0.114 (0.022)	0.13
1977	0.158 (0.067)	0.014 (0.013)	19.00
1978	5.176 (0.433)	0.115 (0.004)	3.33
1979	2.939 (0.653)	0.114 (0.012)	8.02
1980	1.791 (0.284)	0.074 (0.007)	12.50
1981	0.321 (0.100)	0.049 (0.012)	6.00
1982	0.579 (0.084)	0.070 (0.006)	1.36
1983	0.329 (0.055)	0.049 (0.007)	1.83
1984	0.596 (0.213)	0.058 (0.015)	17.10
1985	0.154 (0.037)	0.041 (0.009)	1.30
1986	4.198 (1.325)	0.090 (0.015)	104.00

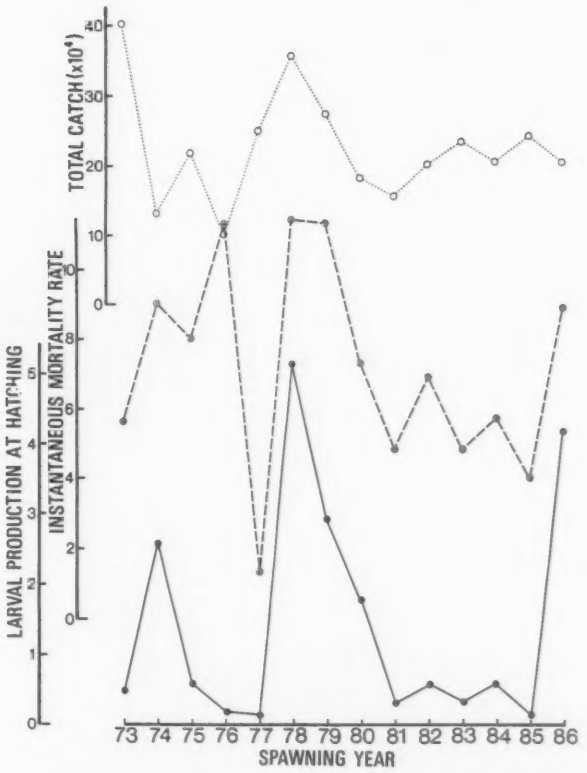

TOTAL CATCH (x10⁴)
INSTANTANEOUS MORTALITY RATE
LARVAL PRODUCTION AT HATCHING
SPAWNING YEAR
73 74 75 76 77 78 79 80 81 82 83 84 85 86

FIGURE 6.—Year-to-year fluctuations of daily Pacific Saury larval production at hatching in number of larvae per tow (——●——), daily IMR (------⊙------), and the annual total catch in metric tons (----○----) of the saury.

think that the downward bias is due to extrusion through the mesh. The mesh retention rate of larvae in the first two size classes could be estimated from the ratio of the observed catch/tow/day and the predicted larval production computed from the overall average mortality curve of 15 years. The estimate of mesh retention rate for larvae of 7.5 mm (3.2 days old) is,

Observed: 0.158 (larvae/tow/day)
Predicted: 0.978 (larvae/tow/day) = 1.255 exp(−0.078 × 3.2)
Retention rate: 0.16 = 0.158/0.978

and for larvae of 12.5 mm (10.5 days old) is,

Observed: 0.345 (larvae/tow/day)
Predicted: 0.553 (larvae/tow/day) = 1.255 exp(−0.078 × 10.5)
Retention rate: 0.62 = 0.345/0.553.

DISCUSSION

Production and mortality rates of fish larvae and juveniles cannot be obtained without good growth models, which are indispensable in calculating stage durations. A new growth model based on growth increments of otoliths has recently been established (Watanabe et al. 1988) enabling calculation of mortality rates. The current results are virtually the first attempt to calculate larval production at hatching. These should provide the best index of reproductive level ever obtained.

Sablin (1978) first calculated mortality rate of juvenile saury for 8 individual years (1968–75), using catch/tow values of two size groups, 26–30 mm and 46–50 mm, and 20 mm/mo as a growth rate of this size range. The average monthly IMR estimated by Sablin was 1.15 with a range from 0.76 to 1.62. He obtained the IMR from 2 size groups for individual years, whereas we used catch data from 9 size classes in computing the IMR. We believe the estimates of IMR reported here are an improvement over those of Sablin.

Monthly mortality rates using the Sablin IMRs (1978) ranged from 53.2% to 80.2% with an average of 68.3%. These values were much lower than the monthly rates calculated from the daily IMRs in this paper, 70.8–96.8% with an average 90.4%. The discrepancy between the two seems to derive from the difference in growth rates used for the computations (Fig. 7). Sablin used a rate of 20 mm/mo (0.67 mm/d) for the size range from 26–30 mm to 46–50 mm. We used the growth model by Watanabe et al. (1988), which shows that sauries grow from 27.5 mm to 47.5 mm in 17.2 days (1.16 mm/d). This was 1.7 times faster than growth rate of Sablin. We recalculated monthly mortality rates using the Sablin IMRs and the Watanabe et al. growth rate of 1.16 mm/d producing estimates close to ours, 73.4–94.1% with an average of 86.5%.

The absolute value of total annual production of newly hatched larvae of the Pacific saury can be calculated from our results using the assumptions that 1) all fish in a vertical water column are in the upper one meter, and 2) those in a volume of water strained are captured by the net during the NIT period. The values of larval production at age 0 are on daily basis over the area covered by a net tow. Thus, the annual total production of the hatched larvae can be computed as below:

$$\text{Annual Total Production of Hatched Larvae} = P_0 \cdot 365 \cdot A/401.3$$

where P_0 is larval production at hatching, A is total spawning area in m^2, and 401.3 is surface area in m^2 covered by one net tow. However, the distribution of saury larvae and juveniles in the northwestern Pacific extends far to the east of Japan, and we cannot delimit the total spawning area. Thus, calculation of the absolute larval production of saury at hatching for the entire area is not practical. However, the calculation of abso-

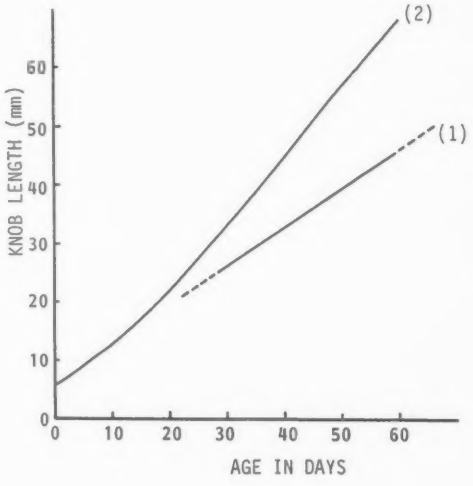


FIGURE 7.—Growth curves used by Sablin (1973) (1) and by us (2) for Pacific saury.

lute larval production in a limited area, which can be covered with a high precision, is possible and will be useful.

The assumption that all the fish in a volume of water strained by the net tow are captured in the NIT period is not realistic for a variety of reasons. The larval net used in this study has bridles in front of the mouth, and to some extent evasion can be expected due to turbulence in front of the net. Visual evasion is possible even in the NIT period because natural waters are not totally dark due to moonlight and a variety of bioluminescent organisms.

Vertical distribution pattern of young sauries has been investigated by towing nets on horizontal strata at several depths (Okiyama 1965; Parin 1967). However, the fraction of the young saury population in the upper one meter available to our net is not known.

The volume of water filtered by a tow may be different among tows depending on wave conditions, mesh clogging, etc. The standardization of catch data by a volume of water filtered must also be done to improve the accuracy of estimates. In our study, we did not have a flow meter with our net. Biases, resulted from these problems, must be resolved before absolute larval production can be obtained.

Unaccounted variances due to the retention correction factor and the duration computed from growth curve could lead to underestimation of the variance of parameter estimates in the mortality curve. On the other hand, the standard error of both P_0 and IMR in the current paper may be higher than the estimates from a regression where each daily fish production estimate is weighted by the inverse of its variance. The effect of the unaccounted variance caused by the retention correction factor could be small because the retention rates were computed from a large number of tows, reducing the standard error of estimated retention to insignificant levels. The variance of duration is unknown. Theoretically it could be estimated from the growth curve, but we did not compute it. A simulation study on evaluating the precision and bias of mortality estimates for northern anchovy (N.C.H.L., unpubl. data) indicated that the variation contributed from bias correction factors is minimal.

We employed an age-independent mortality model in this paper. This does not necessarily mean that the mortality of saury larvae is age-independent. Because of biased catch data due to mesh extrusion in the smallest two size classes, we could not use these two values. This might have had some effect on choosing a mortality model. For further studies we have devised a cylinder-conical larval net for saury that is constructed with one type of mesh (0.53 mm). The body depth at the pectoral fins in early post-yolk-sac larvae is 0.6–0.7 mm, so the new net is expected to retain larvae of the smallest size classes. Thus, the net will enable us to get an unbiased sample of early larvae, and the use of a data set of all size classes including 7.5 and 12.5 mm classes might cause a shift of the mortality model from age-independent to age-dependent type.

Because mortality is a necessary piece of information for computing mean age for each size group, we used the ages corresponding to the midpoints of the size classes for the mortality computation instead of mean ages. It is acceptable to use the midpoint to convert size to age when the mortality information is unavailable, when mortality is low, or when the size interval is small. Bias resulted from the use of the midpoint was large for the first size class: 2.4 days with mortality correction assuming the IMR = 0.08 and 3.2 days using the midpoint 7.7 mm. However, the first two size classes were not included in the mortality computation, so bias caused by using the midpoints was minimal.

The high production values in large juvenile classes (Table 2, Figs. 4, 5) may be due to an underestimation of the durations of these size classes. Year-to-year variations of growth may be large enough to cause considerable differences in durations. The standing stock of larvae in a size class is influenced by the duration of growth through that size class. Because an accurate mortality estimate depends on accurate growth rate estimates, calculation of the growth rate every year, or at least every time the fish size composition changes, is necessary to obtain accurate mortality rates for individual years.

As shown for the northern anchovy, direct estimates of spawning biomass from an ichthyoplankton survey can be obtained (Lasker 1985). This method can be applied to other fishes that produce pelagic eggs. However, the saury produces adhesive eggs and quantitative sampling of them is difficult. Larval census is so far the best index for spawning biomass of the saury. Even if it were possible to obtain quantitative samples of eggs, uncertainties in embryonic mortality rates may rule out use of egg production. The saury has a long incubation time of about 2 weeks under 13°C (Yusa 1960), and slight differ-

ences in the daily mortality rates of embryonic stages, rather than egg production, could have profound influence on larval production at hatching. In other words, larval production at hatching may not necessarily be accurately related to egg production without knowing mortality rates of embryonic stages. Although crude estimation of spawning biomass by conventional plankton tows might be possible (Smith et al. 1970), a radical departure from the egg sampling method using information on vertical and horizontal distribution patterns of the eggs is required to devise an egg production method for the saury.

Lo (1985) calculated the time series of egg production at fertilization of the northern anchovy in 1951–82. Year-to-year difference in the egg production was more than 1,000-fold, which is much larger than the difference in saury larval production at hatching in our study, about 33-fold. She also calculated mean yolk-sac larval abundance for the years that showed a difference of more than 1,000-fold. Annual fluctuation of reproductive level in the saury seemed to be smaller than the northern anchovy. This might be related to the differences in spawning ecology of these two species. The saury is reported to be a multiple spawner that spawns in 2 mo intervals in the spawning season (Hatanaka 1955) with a batch fecundity of 500–3,000 egg/female (Hatanaka 1953). The spawning frequency is 3–5 times/yr and the annual fecundity is estimated to be 1,500–15,000. In contrast, time between spawning incidence of the northern anchovy off southern California is 6–8 days and the batch fecundity is 389 eggs/g of ovary free female body weight (Hunter and Goldberg 1980). The saury is less fecund than the northern anchovy and seems to be less variable in its annual fecundity owing to a long maturation period of ovarian eggs. Small year-to-year differences in the reproductive level in the saury might be the result of less variable spawning effort.

The correlation of the larval production at hatching and the daily IMR in the individual years may indicate that the mortality of young saury is density dependent. Watanabe (1987) showed an inverse correlation between the egg abundance and the overall survival rate of larval and juvenile Japanese sardine up to 1 yr old. He further examined correlations between the egg abundance and the biomass of larvae of the 40 mm size class, and between the biomasses of the 40 mm size class and of the 1 yr recruit size class. He found that egg abundance and survival rate up to 40 mm size class are inversely correlated, whereas the biomass of the 40 mm and 1 yr size class are positively correlated. His conclusion was that the mortality rate of larval sardine is density dependent up to 40 mm. Thus, in some pelagic fish, mortality rates of early life stages could be density dependent.

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Bluefin Tuna, *Thunnus thynnus*, Larvae in the Gulf Stream off the Southeastern United States: Satellite and Shipboard Observations of Their Environment

Michael F. McGowan and William J. Richards

ABSTRACT: The primary spawning area of the western Atlantic stock of bluefin tuna is presumed to be in the Gulf of Mexico. However, bluefin tuna larvae were collected in April and May 1985 along the shelf edge from Palm Beach, Florida to Cape Fear, North Carolina and offshore as far as 260 km east of Jacksonville, Florida over the Blake Plateau. Satellite and shipboard sea-temperature data indicate that the larvae over the shelf edge were advected there in meanders of the Gulf Stream. Bluefin larvae previously reported in the Straits of Florida and off Cape Hatteras were also in the Gulf Stream according to retrospective analyses of temperature and salinity data. Based on age-length relationships and current velocity, one small larva was probably spawned north of Miami, Florida while others could have been advected into the Gulf Stream from the eastern Gulf. Spawning by a few unspent migrating adults could also account for some bluefin larvae in this region. The estimated total larvae off the southeastern United States in 1985 could have been produced by 5% of the spawning stock. Bluefin larvae were found within a narrow range of sea surface temperatures and salinities at offshore stations. Preliminary assessment of larval habitat indicates that waters off the southeastern United States are unfavorable for growth and survival of bluefin larvae relative to hypothesized larval retention areas in the Gulf of Mexico.

The western Atlantic stock of bluefin tuna, *Thunnus thynnus*, spawns from about mid-April to mid-June in the Gulf of Mexico, based on seasonal and areal distribution of their larvae (Richards 1976, 1977). Bluefin tuna larvae have also been collected in the Straits of Florida north of Cuba and east of Miami (Richards and Potthoff 1980; Brothers et al. 1983) and off Cape Hatteras, NC (Berrien et al. 1978).

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Fishery Bulletin, U.S. 87:615–631.

Surveys of the Gulf of Mexico for bluefin tuna larvae are made annually during the spawning season to estimate the total abundance of larvae and to calculate a fishery-independent index of adult spawning stock size (Richards et al. 1981; McGowan and Richards 1986). This index of stock size is used to calibrate virtual population analysis (VPA) of the western Atlantic bluefin tuna population to enhance management of the stock (Anonymous 1986). Fishery catch statistics and the index of abundance of larvae show that the bluefin tuna population size is smaller than it was previously, and is below optimum levels (Brown and Parrack 1985; McGowan and Richards 1986). To redress this problem, directed fishing on bluefin in the Gulf of Mexico and in other spawning areas, has been prohibited since 1982 (Anonymous 1987).

Finding bluefin larvae outside the primary spawning areas raises a potential problem because if significant spawning of the remaining stock occurs outside the Gulf of Mexico, then the ichthyoplankton survey in the gulf may not give a reliable index of the stock, and prohibition of fishing in the gulf may not have the desired effect on stock recovery. In 1985 bluefin larvae were widely distributed off the southeastern U.S. coast. The hypothesis that they were spawned in this area needed evaluation.

In this paper we quantitatively describe the occurrence of bluefin tuna larvae in 1985 near Miami and Cape Hatteras, where they have been reported before, and also their occurrence over the Blake Plateau north of the Bahamas Islands, where they have not been reported previously. We use satellite observations of the position of the Gulf Stream and shipboard hydrographic measurements to describe the habitat where bluefin tuna larvae were collected. We review previous evidence for bluefin tuna spawning in this area to determine if these larvae were in similar, oceanographically defined habitat, and summarize this evidence to assess the waters of the southeastern U.S. coast and the Blake

Plateau as a spawning area for bluefin tuna. We propose a hypothesis, based on existing data, that bluefin tuna are dependent on a dynamic larval retention area associated with the Loop Current in the eastern Gulf of Mexico.

The total number of specimens of bluefin tuna larvae on which this paper is based is small. Therefore, we present our conclusions as hypotheses that are consistent with our data from independent sources and with all other data known to us. Arguments supporting our hypotheses and their limitations will be elaborated in the discussion.

Our investigations were initiated by the observation of bluefin tuna larvae outside the normal spawning area and then proceeded by a series of questions, critical examination of available information, and conclusions and hypotheses for further investigation. The bluefin tuna larvae off the southeastern U.S. in 1985 could have been spawned locally or transported in currents. Were they in water masses characteristic of the Gulf Stream? If they were in the Gulf Stream, then were they young enough to have been spawned locally or were they transported from upstream? Other researchers had reported incidental catches of bluefin tuna larvae in some of the same areas. Were these larvae likely to have been spawned locally? Wherever they were spawned, could they survive where they were collected? What were the general temperature-salinity conditions where bluefin tuna larvae were found off the southeastern U.S.? Are these conditions similar to those which bluefin tuna larvae experience in the Gulf of Mexico? What else is known about the oceanography of this region which is relevant to survival of fish larvae? Given our conclusions from these data and our knowledge of the life history of the bluefin tuna, what insights can be drawn from the occurrence of larvae outside the presumed spawning area and what hypotheses need to be tested by additional work?

METHODS

Ichthyoplankton were collected on cruise 152 of the RV *Oregon II* in April and May 1985. Double oblique tows to 200 m or to near the bottom in shallow water were made with 0.6 m diameter bongo nets having 0.333 mm mesh size. Bluefin tuna larvae were identified and measured by W. J. Richards. Salinity and temperature data collected by CTD, XBT, or bottle cast at each station were extracted from computer data files of the National Marine Fisheries Service, Mississippi Laboratory, Pascagoula. Satellite data for April and May 1985 were obtained from NOAA Miami SFSS Gulf Stream Position Flow Chart #2450 for the days during the cruise. Historical observations of bluefin tuna larvae and coincident temperature and salinity near Cape Hatteras were obtained from Berrien et al. (1978) and Clark et al. (1969). Previous observations of bluefin tuna larvae outside the Gulf of Mexico were reviewed for other evidence of spawning in the Straits of Florida or elsewhere (Richards 1976; Brothers et al. 1983).

Statistical estimates of standardized abundance of larvae were made using the delta-distribution, an efficient estimation technique when zero counts are observed (Pennington 1983). This is the same method routinely used to construct the fishery-independent index of the abundance of Gulf of Mexico spawners. Because of logistical and statistical sampling problems, the estimates of abundance are best regarded as indices calculated in a consistent way and valid for comparative purposes. Unless there is spatial periodicity or patchiness at the same scale as our sampling grid, the systematic survey does provide, however, an accurate estimate of mean abundance and its variance (Poole 1974; Ripley 1981). The details of the method are provided in McGowan and Richards (1986). The estimate assumed that fecundity, sex ratio, spawning season, and length-weight-age ratios were the same off the southeastern U.S. as in the Gulf of Mexico (Baglin 1982). This assumption was supported by the similarity of length-frequency distributions of incidental catches of adults in the two areas during May 1985. Because our assumptions are important to subsequent arguments, the evidence substantiating our reasoning is given in detail below.

Approximately 90% of incidentally caught adult bluefin tuna in the gulf and off the southeastern U.S. during May 1985 were large, spawning-sized fish >190 cm (data provided by S. Turner, National Marine Fisheries Service, Miami Laboratory). There was no statistical difference in proportion of adult spawners between the two areas (Chi-Square = 0.0176; $P = 0.89$; McGowan and Richards 1987). Thus the available catch data were consistent with our assumption that the fish in both areas were similar in terms of size-related reproductive capacity. This was the primary justification for using reproductive parameters of Gulf of Mexico tuna for calcu-

lations of potential stock size of spawners off the southeastern U.S.

Additional data indicate that there is only one spawning stock in the northwestern Atlantic. Bluefin tuna are known to occur in different places at different times of the year, depending on size and age (Rivas 1978; Mather 1980). The large adults are expected to be migrating through the Straits of Florida during late April and May after spawning in the Gulf of Mexico. A few migrating, ripe females and recently spent males were caught in May near Bimini in the Bahamas (Rivas 1954). Bluefin tuna are capable of swimming from the Bahamas to Norway at sustained speeds as fast as 122 miles per day (Brunenmeister 1980), so adult fish could easily traverse the area from Miami to Cape Hatteras, or be widely distributed over the Blake Plateau, a few days after leaving the Gulf of Mexico. They could migrate back and forth between the two areas during the 60 d spawning season, although there is no evidence for this. Because there is no evidence for two separate groups of spawning fish, the parsimonious assumption is that there is only one. Therefore we assumed that fish in both areas had the same reproductive parameters previously estimated (Baglin 1982; McGowan and Richards 1986).

The estimated age-at-length of bluefin tuna larvae was based on previous analysis of daily increments in otoliths of larval bluefin collected from the Gulf Stream near Miami (Brothers et al. 1983). We calculated a linear regression to predict age from length using the mean estimates of age at length presented in Brothers et al. (1983). The equation is

$$\text{Age (days)} = 3.67 \times \text{standard length (mm)} - 8.04.$$

This equation was based on limited ranges of age and length, so we used it heuristically as the best available. It may be revised after further study extends the age and length data, but the revisions will most likely be at the older-longer end of the relationship, not at the younger-shorter end most relevant to our conclusions in this paper. There is a range of age at length which could affect interpretations of time spent drifting by the larvae but our use of the mean results in conservative interpretations of the data in most instances.

In this paper we refer to the current from the Dry Tortugas to Cape Hatteras as the Gulf Stream (Iselin 1936; Stommel 1965). We refer to the continental shelf area between Palm Beach, FL and Cape Hatteras, NC as either the region off the southeastern United States, or the South Atlantic Bight.

Stations occupied during RV *Oregon II* cruise 152 were numbered 42XXX, where XXX is a sequential station number. For brevity we refer to stations in this paper by their unique 3 digit number, the XXX part.

RESULTS

Catch and Abundance of Larvae

Larval bluefin tuna were collected at 10 of 147 stations during cruise 152 (Fig. 1). Three larvae were collected at one station, two at two stations, and one each at the other positive stations for a total catch of 14 larvae (Table 1). To put this small catch in perspective, in 1984 and 1986 the average catch in the Gulf of Mexico was less than 24 total larvae at 10 positive stations (McGowan and Richards 1987). Thus the 14 caught in 1985 could have been over 50% of the expected catch for the Gulf of Mexico in 1985. The larvae ranged in length from 3.0 to 6.2 mm corresponding in age from 3 to 14.7 days postfertilization. The estimated mean abundance of bluefin tuna larvae from stations at or outside the 183 m isobath was 0.383 ± 0.114 (SE) under 10 m^2 of sea surface (approximately ⅓ the density of bluefin larvae in the Gulf of Mexico). The corresponding area surveyed was 2.02×10^{11} m^2 producing a total estimated 7.74×10^9 larvae in the survey area. These larvae could have been produced by 3,730 adult fish weighing a total of 903 t. This is equivalent to about 5% of the 1985 estimate of Gulf of Mexico spawning stock calculated from the larval index (McGowan and Richards 1987). The coefficient of variation of the estimate of abundance of these larvae was 30%, which is in the range of coefficients of variation for the Gulf of Mexico for the past 10 years, 21–49% (McGowan and Richards 1987).

Distribution of Bluefin Tuna Larvae and Coincident Water Masses

There were three groups of stations where bluefin tuna larvae were present: 1) three stations at the shelf break east of Florida, 2) two stations near the shelf break off North Carolina, and 3) the positive stations over the Blake Plateau. The stations in the first group (634, 636, and 647) were near the 183 m isobath. Two inde-

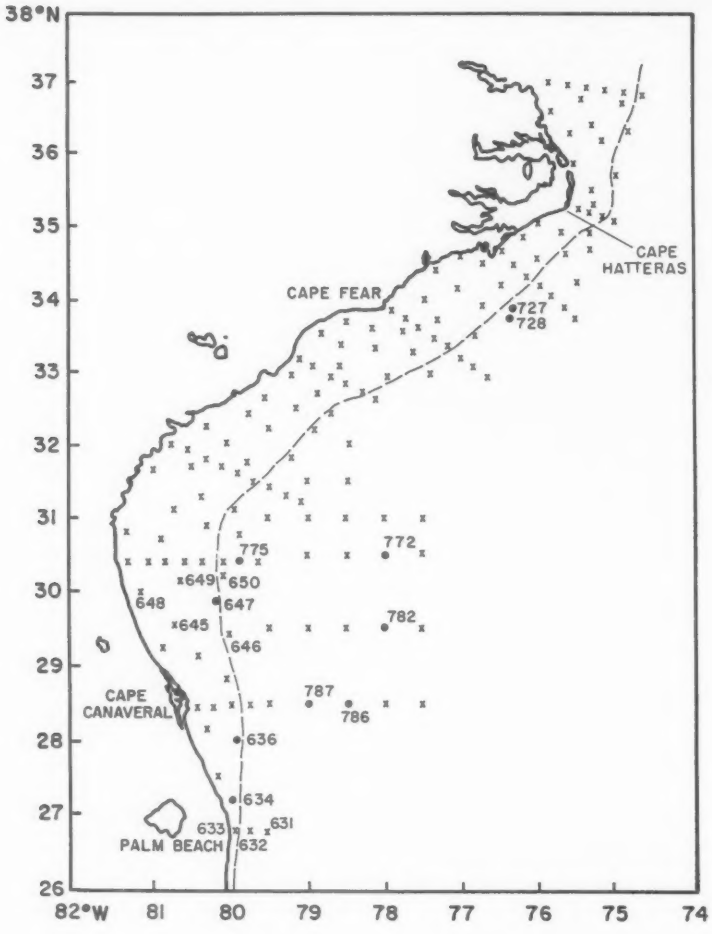

FIGURE 1.—Study area with ichthyoplankton and hydrographic stations plotted, and selected stations numbered. Stations where bluefin tuna larvae were present are indicated by a heavy dot. The dashed line shows the position of the 183 m isobath.

pendent sets of data, temperature-depth profiles, and remote sensing images of surface temperature, show that the water at these stations when bluefin tuna larvae were caught was the shoreward edge of the Gulf Stream. Temperature profiles of stations 631, 632, and 633 (Fig. 2) show cold water is closer to the surface at the inshore station (633) than at the offshore stations (631, 632). This is typical at the cold edge of the Gulf Stream near the shelf break (e.g., Atkinson 1985). Station 634, where bluefin tuna larvae were present, is a little inshore and north of station 633. Its vertical temperature profile shows warm Gulf Stream water at the surface and the cold water of the edge of the stream closer to the surface than at station 633. Station 636, where bluefin tuna larvae were present also, has a similar temperature profile. The upper mixed layer at stations 634 and 636 is approximately 30 m deep like that at station 633, not 60–80 m deep as at station 631 which was farther offshore. These temperature profiles are typical of the edge of the Gulf Stream at this latitude (Atkinson et al. 1987).

The third positive station in this group of stations at the shelf edge is station 647. No observations of temperature with depth were obtained at this station but measurements at adjacent

TABLE 1.—Stations where bluefin larvae were present on *Oregon II* Cruise 152, April and May 1985.

Station	Date	Time	Latitude	Longitude	Depth (m)	Catch	Length (mm)
42634	4/27	1035	27°10.5′	79°51.1′	70	1	4.0
42636	4/27	1732	27°58.2′	79°59.6′	122	3	5.6
							6.1
							6.2
42647	4/29	524	29°51.9′	80°12.3′	210	1	3.8
42727	5/14	1043	33°51.0′	76°17.0′	366	1	5.8
42728	5/14	1445	33°44.0′	76°19.0′	561	1	3.0
42772	5/21	2200	30°30.0′	78°0.0′	842	2	3.0
							4.2
42775	5/22	900	30°24.0′	79°39.0′	732	1	5.7
42782	5/23	1515	29°30.0′	78°0.0′	843	1	4.0
42786	5/24	1100	28°30.0′	78°30.0′	950	1	4.5
42787	5/24	1314	28°30.0′	79°0.0′	846	2	3.7
							4.9

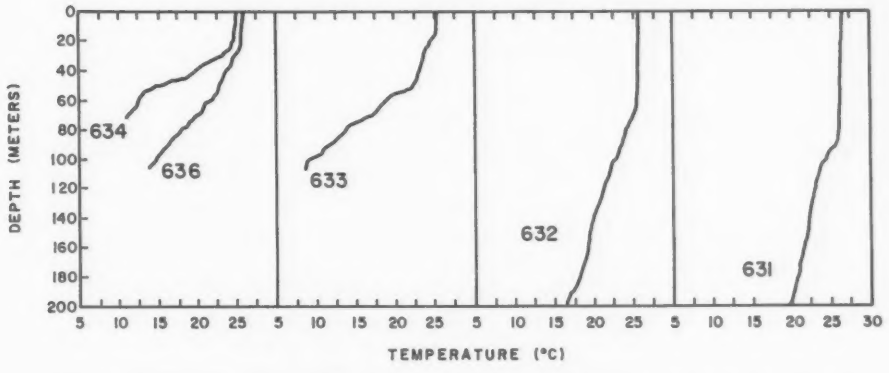

FIGURE 2.—Temperature-depth profiles of selected stations in the southern part of the study area. Stations 631, 632, and 633 are along an east to west transect at the edge of the shelf (see Figure 1). The edge of the Gulf Stream is indicated by colder water near the surface inshore at station 633. Bluefin larvae were collected at stations 634 and 636 where the profile is similar to that at 633.

stations are useful as proxies. Station 646, which was south and a little offshore from 647, shows a vertical temperature profile (Fig. 3) typical of the Gulf Stream, similar to that at 631 (Fig. 2). Station 650, at a similar isobath and distance from the shore, also shows a temperature profile similar to 631 and 632. Therefore station 647 would reasonably be expected to be more similar to 646 and 650 than stations 648, 645, and 649, which are farther inshore. These temperature profiles indicate that Gulf Stream water was present at stations 634, 636, and 647 when bluefin tuna larvae were collected there.

This conclusion is supported further by charts of satellite data showing the position of the edge of the Gulf Stream. The edge of the stream was just offshore of the 183 m isobath on 26 April, the day before the bluefin tuna larvae were collected at stations 634 and 636 (Fig. 4). The edge was inside the 183 m isobath and inshore of the three stations three days later on 29 April, when bluefin tuna larvae were collected at station 647 (Fig. 5). The satellite-detected temperature front associated with the inshore edge of the Gulf Stream is known to be in accord with the classical definition of the stream path (Olson et al.

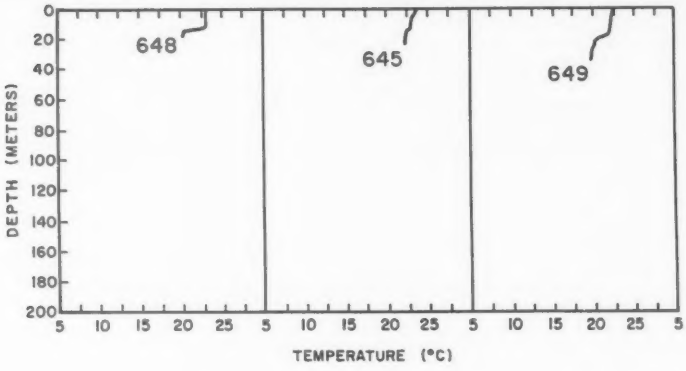

FIGURE 3.—Temperature-depth profiles of stations 646 and 650, which are presumed to represent the profile at station 647. Bluefin larvae were collected at 647 but no hydrographic data were collected there. Profiles for

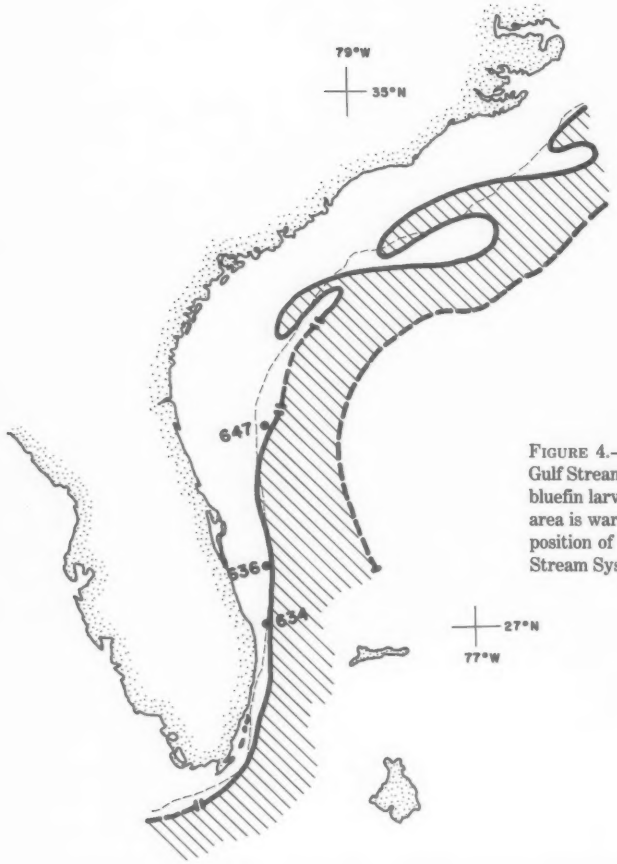

FIGURE 4.—Chart showing the position of the edge of the Gulf Stream on 26 April 1985 relative to three stations where bluefin larvae were collected 27–29 April. The cross-hatched area is warm Gulf Stream water. The dashed line shows the position of the 183 m isobath. (Redrawn from NOAA Gulf Stream System Flow Chart #2450, 26 April 1985.)

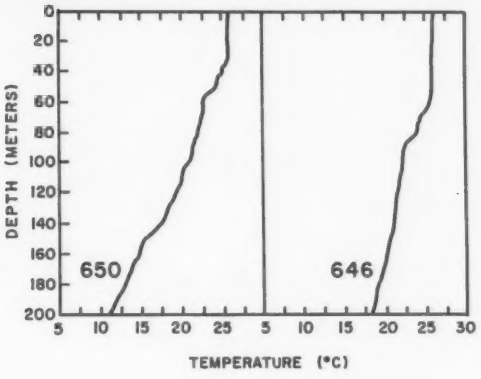

FIGURE 3.—*Continued*—stations 645, 648, and 649, are presumed not to represent conditions at 647 because they are farther inshore.

1983). The inference to be drawn from this remote sensing data is that during 27–29 April the Gulf Stream meandered inshore of the 183 m isobath in this region carrying bluefin tuna larvae over the shelf edge. This is worth noting with regard to the larval habitat of the bluefin tuna because the larvae are rarely taken in water <200 m deep. For example, in the Gulf of Mexico during 1977–81 only 5 of 81 stations that had bluefin tuna larvae were in water <200 m deep and none was in water <110 m deep. (Southeast Fisheries Center, National Marine Fisheries Service, unpubl. data.)

The second group of stations where bluefin tuna larvae were caught is the pair of stations east of Cape Fear, NC where the water depth was 360–560 m (stations 727 and 728). Water temperatures at the surface, at 100 m, and at 200 m were similar to temperatures at the same depths for other Gulf Stream stations such as

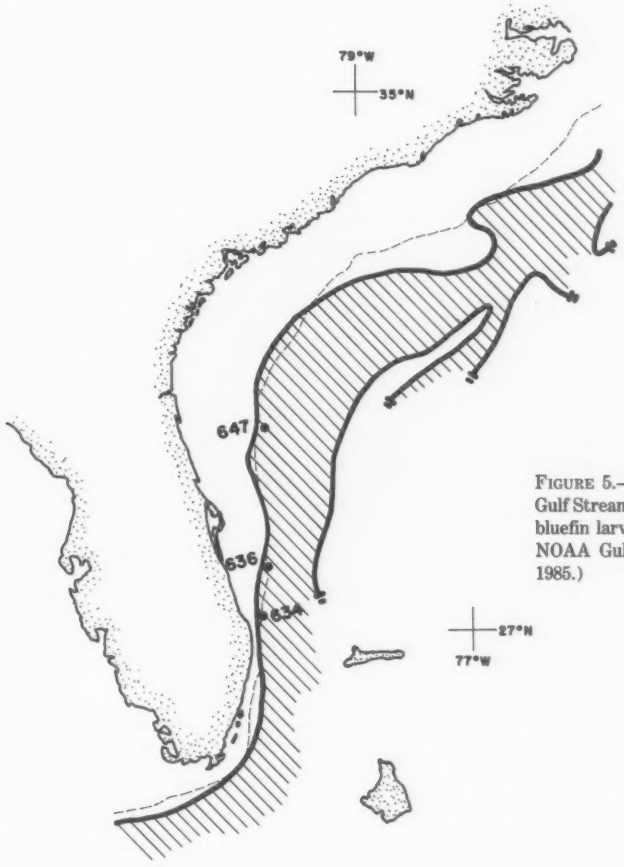

FIGURE 5.—Chart showing the position of the edge of the Gulf Stream on 29 April 1985 relative to three stations where bluefin larvae were collected 27–29 April. (Redrawn from NOAA Gulf Stream System Flow Chart #2450, 29 April 1985.)

station 631 and 632 (Table 2). Station 727 was located at a shallower isobath than station 728 and the temperature at depth readings were similar to those 800 km south, at stations 632 and 631, where the water depth was similar. At both pairs of stations cold water is nearer the surface of the inshore station. The sloping isotherms and the temperatures at depth are characteristic of the edge of the Gulf Stream. Gulf Stream water is expected here in spring and summer (Pietrafesa et al. 1985).

Remote sensing observations (Figs. 6, 7) show that remnants of a filament of warm water resulting from an earlier onshore meander were still present when these larvae were collected. Upwelling is associated with onshore meanders of the Gulf Stream and cyclonic eddies are formed between the warm filament and the Gulf Stream. The bluefin tuna larvae at stations 727 and 728 were not over the shelf in a patch of productive water caused by the onshore meander, but they were in an area which could have been fertilized by such a patch which subse-

TABLE 2.—Temperature with depth comparison of northern stations where bluefin larvae were present and southern stations which were at the same isobath and in Gulf Stream water. Bluefin were collected at stations 727 and 728. Stations 728 and 631 were offshore (Fig. 1.). Note that 22° at 100 m is a good indicator of the Loop Current (Liepper 1970) which flows from the Gulf of Mexico to join the Gulf Stream.

	Temperature (°C)			
	Northern stations		Southern stations	
Depth (m)	727	728	632	631
0	25.8	26.2	26.1	26.8
100	21.8	22.5	21.6	23.6
200	16.7	19.2	16.7	19.5

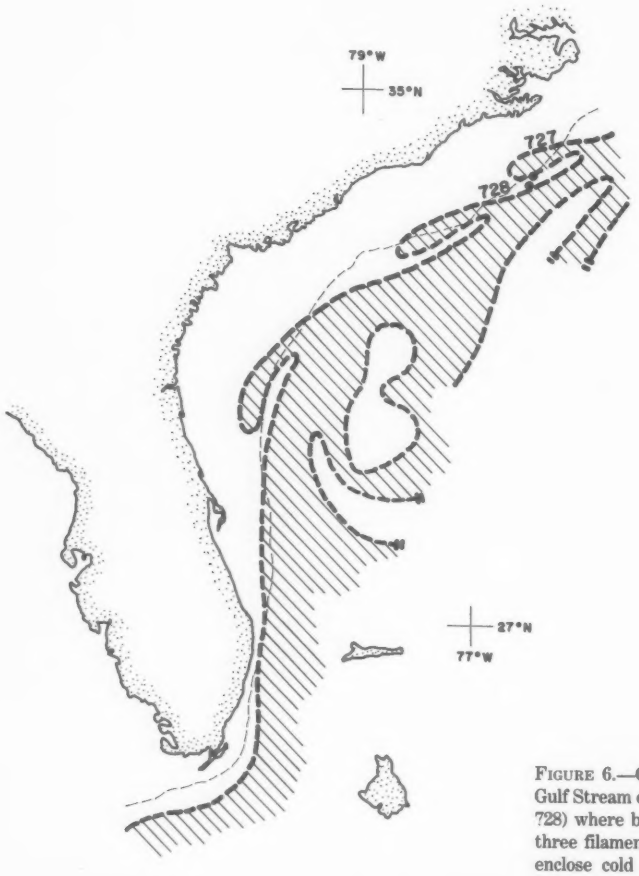

FIGURE 6.—Chart showing the position of the edge of the Gulf Stream on 13 May 1985 relative to two stations (727 and 728) where bluefin larvae were collected 14 May. Note the three filaments left by meanders of the Stream. These can enclose cold cyclonic eddies. (Redrawn from NOAA Gulf Stream System Flow Chart #2450, 13 May 1985.)

quently moved offshore. A 3.0 mm bluefin larva estimated to be only three days old was collected here at station 728.

The third group of stations with bluefin tuna larvae were all farther offshore in water more than 700 m deep. The surface water here had a narrow range of salinities from about 36.0 to 36.5 ppt. Temperature at the surface in this region ranged from approximately 24.5° to 27.5°C. Bluefin tuna larvae were found where the surface water was in the center of this temperature range: from 25.5° to 26.5°C. Bluefin tuna larvae from the northern positive stations and the southern shelf edge stations were also found at the same surface salinities and temperature, except for station 634 where the temperature was 24.8°C (Fig. 8).

Previous Captures of Bluefin Tuna Larvae off Cape Hatteras

In 1966 three bluefin tuna larvae were collected off Cape Hatteras (Berrien et al. 1978). One larva 7.7 mm long was collected 20 April in 235 m water depth. Two larvae, 5.4 mm and 9.3 mm SL, were collected 23 June over 269 m and 68 m, respectively. The stations where these larvae were collected are at the shelf edge or just inshore of it. Contour plots of surface temperature (Fig. 9) and salinity (in Berrien et al. 1978) show that the Gulf Stream front was inshore of the stations where bluefin larvae were caught. Temperature cross-sections show clearly that the stations where bluefin tuna larvae were collected were in Gulf Stream water (Fig. 9). The larva caught in April was in water with lower surface temperature and lower surface salinity than typical (Fig. 8) for the stations where bluefin tuna larvae were present in 1985. The two larvae caught in June were in water more typical for bluefin tuna larvae but near the highest salinities and temperatures (Fig. 8).

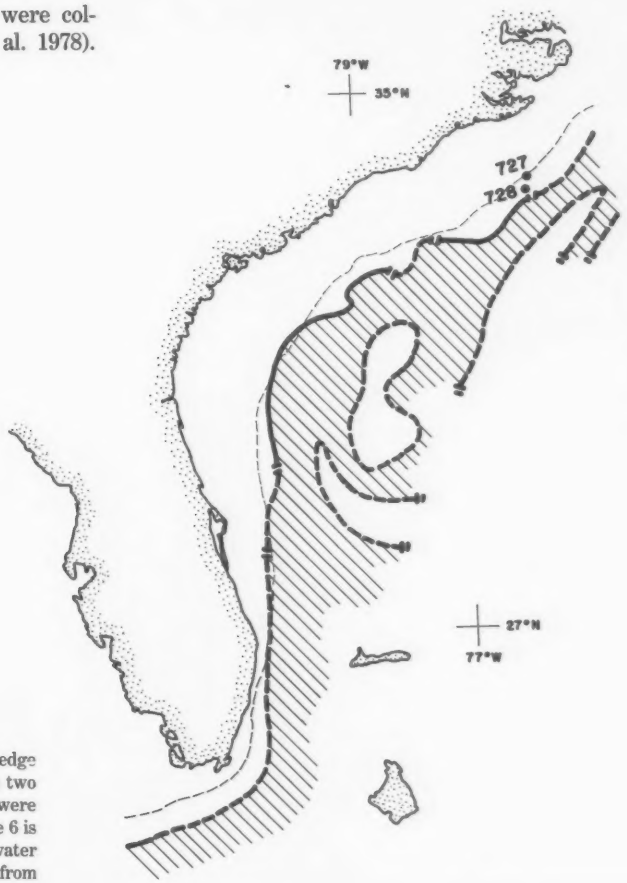

FIGURE 7.—Chart showing the position of the edge of the Gulf Stream on 15 May 1985 relative to two stations (727 and 728) where bluefin larvae were collected 14 May. The filament shown in Figure 6 is not visible and the stations are now in colder water inshore of the edge of the Stream. (Redrawn from NOAA Gulf Stream System Flow Chart #2450, 15 May 1985.)

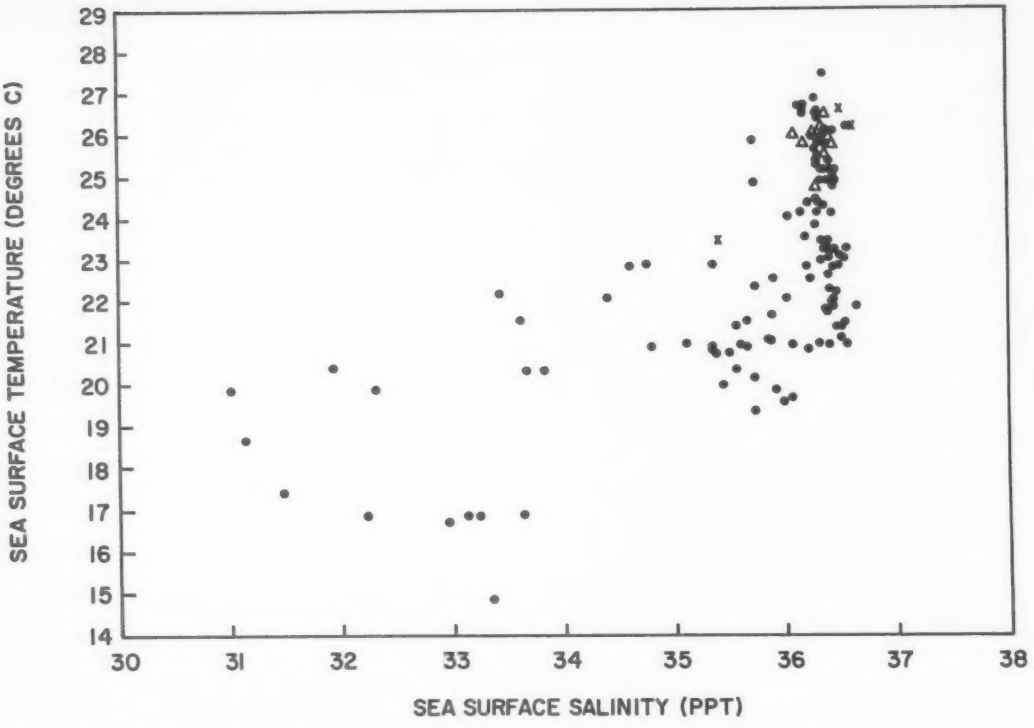

FIGURE 8.—Plot of sea surface temperature vs. sea surface salinity for stations on the cruise which had observations of both. Stations with bluefin larvae are plotted as open triangles. The three x's show the surface temperature and salinity of the stations near Cape Hatteras where bluefin larvae were collected by Berrien et al. (1978).

Previous Captures of Bluefin Tuna Larvae off Miami

Bluefin tuna larvae were collected in 1969–71 and in 1975 between Miami and the Bahamas by Richards (1976). On a five-station transect between Miami and Bimini Bahamas (Richards 1976, table 2), 82% (32/39) of bluefin tuna larvae taken in neuston tows were taken at two stations. These two stations were located on the Miami side of the center of the Florida Straits where the high velocity core of the current is located on average (e.g., Stommel 1965:139). All of the bluefin tuna larvae taken in bongo tows along the transect were taken at the same two stations where most of the neustonic specimens were collected. All of these larvae were longer than 3.0 mm, older than 3 days, so that, if they were advected at the mean current velocity in this location, 100 km d^{-1} (Fuglister 1951), they would have been spawned west of Key West, FL (long. 82°W).

In 1981, 369 bluefin tuna larvae were collected off Fowey Light, south of Miami, at approximately lat. 25.6°N (Brothers et al. 1983). The collections were made on four days, 19–21 May and 2 June, using 1 m diameter or 1 × 2 m neuston nets which were towed many times each day. No oceanographic data were collected because the purpose of the sampling was to capture specimens for otolith ageing, but the collections were made "5–10 miles offshore in blue water at the edge of the Stream" according to E. D. Prince.[1] Based on satellite observations during this period (NOAA Gulf Stream System Flow Chart #2450), the edge of the Gulf Stream was offshore of the 183 m isobath (which is 5–10 miles offshore near Fowey Light) on 18 May, was at the 183 m isobath 20 May, and was offshore again 22 May. Nearly half of the total catch (176/369) of bluefin tuna larvae during four days of sampling took place on 20 May (Brothers et al.

[1]E. D. Prince, Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149, pers. commun. 1988.

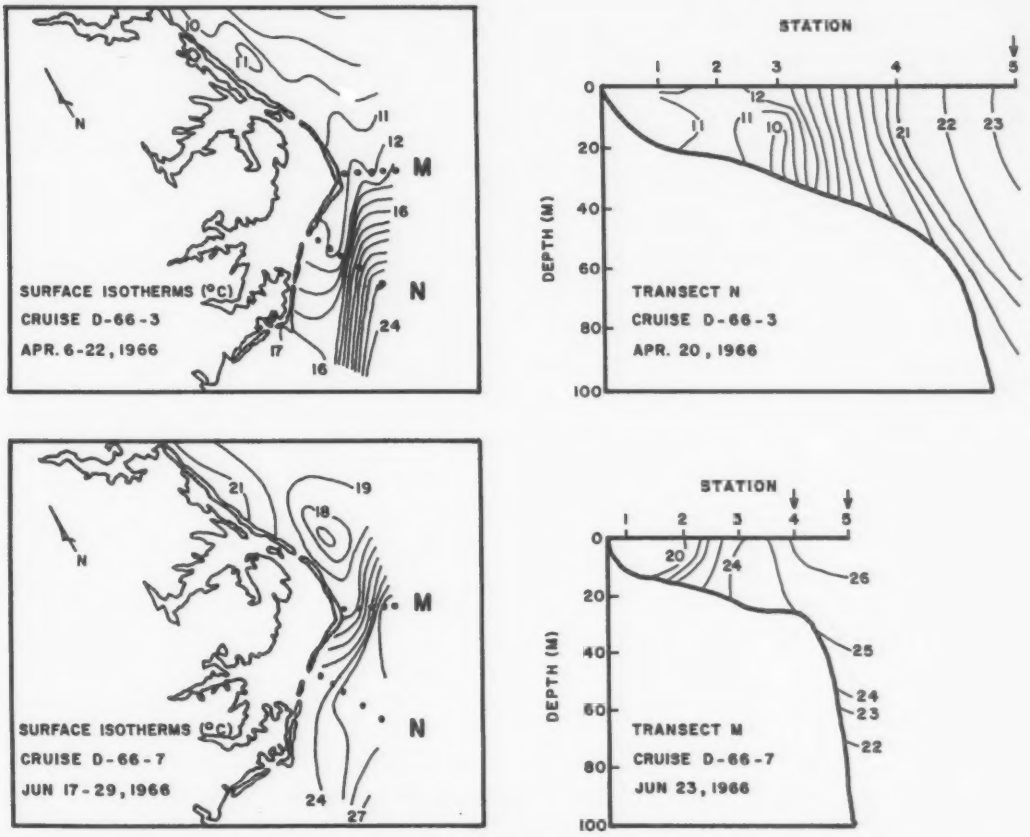

FIGURE 9.—Plots of surface isotherms and temperature sections of the stations where bluefin larvae were collected near Cape Hatteras by Berrien et al. (1978). The plot at upper left shows the position of the temperature front at the sea surface between stations 3 and 4 on transect N. The section at upper right shows that the front extends to the bottom; station 5, where a bluefin larva was collected, is indicated by an arrow. Plot at lower left shows the surface front inshore of station 4 on transect M. Section at lower right shows temperatures; the two stations where bluefin larvae were caught are indicated by arrows. (Figures redrawn from Berrien et al. 1978.)

1983:50), the day when the Gulf Stream was at its closest inshore position during the sampling days. Thus nearshore catches were highest when the rapidly flowing core of the Gulf Stream meandered toward shore, carrying bluefin tuna larvae with it.

DISCUSSION

Limitations of the Data

Bluefin tuna larvae are rare on the average in their oceanic habitat. Standard ichthyoplankton tows, which are made to 200 m in order to quantitatively sample all species, undersample the surface layers where tuna larvae are more abundant. In addition, we have evidence, to be published elsewhere, that bluefin tuna larvae are most abundant near specific oceanographic features; so they may be undersampled by nonstratified survey designs such as the uniform grid often used for logistical reasons. The estimates of abundance will be valid but may have wider confidence intervals than estimates made with a more efficient stratified design. Furthermore, bluefin tuna larvae grow and swim rapidly, so they avoid plankton nets better than larvae of most other species, again contributing to low absolute catches. We acknowledge that low catches limit the precision of results; therefore, we tried to rein in unwarranted speculation. The calculations of adult biomass from larval abun-

dance are made only for comparative purposes. A recent independent review of our techniques concluded that the index of larval abundance probably reflects trends in abundance of adults accurately but that our ad hoc estimate of adults from the larvae resembles VPA estimates coincidentally because of our choice of a larval mortality rate. Our ongoing research is aimed at improving the precision and accuracy of estimates of abundance of bluefin tuna larvae by combining our increasing knowledge of their biology with improved sampling gear and methods.

Nevertheless, we are confident that our interpretation of the preceding data is justified and reasonable because of decades of accumulated experience with this species, because of the variety of independent sources of data which are consistent with our interpretations, and principally because the most important conclusions and hypotheses presented here are not dependent upon quantitative estimates of abundance, but upon the relationship between presence and absence of bluefin tuna larvae with specific oceanographic variables. Despite our confidence in our presentation of the results we readily admit that additional data could falsify our conclusions.

Assessment of Spawning off the Southeastern United States

Assuming that all the larvae caught near the shelf and over the Blake Plateau were spawned near where they were collected, spawning in the area was only a small fraction (5%) of estimated total spawning by the western Atlantic stock (McGowan and Richards 1987). This is similar to a previous estimate (6%) of the number of ripe females passing the Bahamas during May (Rivas 1954:310). However, because of the currents in this region, it is not certain that the larvae were spawned near the area where they were collected.

Currents along the outer shelf off the southeastern U.S. average 0.5–1.0 m s^{-1} during the summer (Atkinson and Menzel 1985). Gulf Stream surface currents off Florida based on ship drift observations during April–June average 1.5 m s^{-1} or less (Fuglister 1951). During April–June 1985 the mean northward current, measured at 29°N and at 30 m depth over the 75 m isobath, was 0.53 m s^{-1} and the maximum current was 1.55 m s^{-1}, approximately 3 kn (Lee et al. 1986). Current velocity at the wind-affected surface and farther offshore in the fastest moving region of the Gulf stream would be higher.

If we use the long-term average of 1.5 m s^{-1} as the mean northward speed of the surface current, then a planktonic fish larva would travel 116 km in one day. The mean distance travelled in 7 days would equal 812 km which is less than the straight-line distance from Cape Hatteras, NC (35°N, 76°W) to Palm Beach, FL (27°N, 80°W), approximately 970 km. These calculations suggest that larvae <7 days after fertilization, which were found as far north as Cape Hatteras, could have been spawned north of the Straits of Florida. Those more than 7 days old, or larger than about 4 mm (minimum size at this age, not mean; see Brothers et al. 1983), could have been spawned in the Straits of Florida or the southeastern Gulf of Mexico. Ten of the 14 larvae collected in 1985 were 4.0 mm or longer, and most of the larvae were caught far south of Cape Hatteras. Therefore, based on current velocity and estimated ages, most of the bluefin tuna larvae were probably not spawned off the southeastern U.S. near the area where they were collected.

The 3 d old (3.0 mm) bluefin tuna larva collected near lat. 34°N could not have been spawned in the Gulf of Mexico because, even at 2.5 m s^{-1}, it would have travelled only 667 km in three days. A 667 km straight line from where the larva was caught would end at about 28°N, which is north of Palm Beach. However, the interpretation must be different for the larger, older larvae. Except for the single 3 mm larva, those in the high velocity core of the Gulf Stream (at the shelf edge) could have been advected from a distance to the south in only a few days. At only 1.0 m 5^{-1} (a little faster than 2 kn) larvae 4–5 mm long, corresponding to approximately 8 days old, could have been advected from off Miami to about 31°N in 5 days. The larvae collected along the shelf edge and over the Blake Blateau in 1985 were in this size range or a little longer. Therefore all but the 3 mm larva could have been spawned in the southeastern Gulf of Mexico or between the Florida Keys and Cuba. Slow growth due to cold-water temperature could explain small larvae far from their spawning area, but in this case the Gulf Stream water was warmer than the water where bluefin tuna larvae were found in the Gulf of Mexico.

It should be noted that the current circulation east and north of the Bahamas is complicated

(Olson et al. 1984). Gyres and slow recirculation in this area could retain fish larvae for several days. This means that the evidence presented here does not eliminate the possibility that bluefin tuna spawn off the southeastern U.S. However, because larvae collected in rapidly moving water were probably transported in that water, we argue that the data support the contention that the primary spawning area is farther upstream with perhaps some late spawning by a few individuals in the Straits of Florida as suggested by Rivas (1954).

Oceanic Habitat of Bluefin Tuna Larvae

Four aspects of larval fish habitat are important to the survival of individuals and recruitment to the adult stock: thermal and salinity conditions, prey, predators, and patterns of ocean circulation that can retain the larvae in favorable areas. Our data do not permit discussing the predators coincident with the bluefin tuna larvae found off the southeastern U.S., but we can discuss the salinity and temperatures, the food potentially available, and the likelihood of retention in a favorable area.

Surface salinity over the shelf of the southeastern U.S. is generally 35 ppt or less, with peak river runoff in spring affecting the central and inner shelf (Atkinson and Menzel 1985). Salinities over the outer shelf are similar to those in the Gulf Stream (35.0–36.5 ppt; Stommel 1965). Salinity lower than full-strength seawater could be potentially detrimental to larval bluefin tuna although the adults tolerate reduced salinities (Topp and Hoff 1971). All the larvae collected in this study were found within a narrow range of salinity near 36 ppt (Fig. 8). The larvae were also found in a fairly narrow range of temperatures near 26°C (Fig. 8). In the Gulf of Mexico in 1984 and 1986, bluefin tuna larvae were found where sea surface temperature (SST) ranged from 22.0° to 28.1°C. More than 87% of the larvae occurred in a narrow range of temperatures between 24.0° and 26.1°C (Southeast Fisheries Center, National Marine Fisheries Service, unpubl. data). This is similar to the temperature range off the southeastern U.S. where bluefin tuna larvae were found at SST's from 24.7° to 26.5°C However, the mean temperature of occurrence of the bluefin tuna larvae was higher here than in the Gulf, 25.72° vs. 24.99°C (t = 2.98; df = 50; $P < 0.005$). At higher temperature metabolic requirements of the larvae would be higher; larvae would require more food for optimal growth and survival, other conditions being equal.

A potential mechanism for producing larval fish food does exist in this region. Onshore meanders of the Gulf Stream along the southeastern U.S. can cause upwelling of nutrient rich water along the shelf edge (Yoder et al. 1981; Yoder 1983). This and the compression of isotherms near the edge of the Gulf Stream might produce a stable stratified region favorable to the growth and to the persistence of patches of larval fish food (Lasker 1981). It is true that intrusions of cold, upwelled water provide pulses of phytoplankton production on the shelf which initiate the formation of patches of zooplankton (Paffenhofer et al. 1987). However, these isolated patches are most often produced in July, when winds as well as currents are favorable for upwelling. Furthermore, the zooplankton in the patches consist primarily of small species of copepod and gelatinous salps and doliolids which are most abundant in cool water near the bottom and in the thermocline. Small copepods are not ideal food for larval bluefin which eat other larval fishes. Larval fishes were not noticeably abundant in the patches; however, the sampling gear used by Paffenhofer et al. (1987) was not optimal to catch fish larvae. The gelatinous zooplankters which can be predators of fish larvae pose a potential hazard to the tuna larvae. Therefore the patches of plankton on the shelf caused by onshore meanders of the Gulf Stream do not appear to be favorable habitat for the feeding or survival of bluefin tuna larvae. These isolated patches on the shelf probably benefit benthic filter-feeders more than larval fishes.

Not all meanders that cause upwelling may result in isolated patches on the shelf. A pulse of upwelled, nutrient rich shelf-break water could move offshore, be entrained in the Gulf Stream, and increase the local productivity of near-surface water, thus enhancing the offshore habitat for larval fishes. Longhurst (1983) suggested that surplus production occurs on continental shelves. Walsh et al. (1987) detected export of phytoplankton from the Mid-Atlantic Bight during a spring plankton bloom. Sherman et al. (1984) found that peak spawning for some species is related to topographic features and circulation, and is synchronized with production of the copepod prey of their larvae. Something about the two stations with bluefin tuna larvae off North Carolina in this study (Figs. 6, 7) may have resembled "good" spawning habitat enough to induce migrating adult bluefin tuna to spawn

nearby. Phytoplankton patches can seed other downstream patches in eddies (Heywood and Priddle 1987). This would be favorable for larval tunas offshore of the Gulf Stream front if these patches produced a food chain containing their prey. Much of the eddy-induced production may be flushed offshore rather than contribute to the shelf food chain (Walsh 1986). However, a pulse of nutrients from shelf-edge upwelling would be diluted rapidly by mixing with the Gulf Stream. We need more quantitative knowledge of the trophic results of these linkages between the shelf break and the Gulf Stream and more information about the food requirements of larval bluefin before the potential benefits of shelf-break upwelling to epipelagic ichthyoplankton can be assessed.

Dynamic Larval Retention Areas

Bluefin tuna larvae have been collected over wide areas of the Gulf of Mexico. They appear to occur primarily where currents or eddies encounter the shelf between the 100 and 1,000 m isobaths (Sherman et al. 1983). They may be most abundant at the cold edge of the Loop Current surface fronts in the eastern Gulf of Mexico (Richards et al. in press). Variability in the Loop Current (Sturges and Evans 1983) will produce variability in the seasonal occurrence and amount of such habitat for the bluefin tuna larvae in the Gulf. The amount of habitat may limit the number of bluefin tuna recruits to the adult stock as has been hypothesized for Atlantic herring stocks (Iles and Sinclair 1982). Because it is outside the rapidly flowing Loop Current which feeds into the Gulf Stream, this habitat may be a larval retention area of bluefin tuna. In the larval retention hypothesis developed for Atlantic herring (Sinclair and Iles 1985), the larvae do not undergo development while drifting passively (e.g., Harden-Jones 1968). Instead, they develop into juveniles within a retention region and then migrate actively to juvenile nursery areas.

Bluefin tuna larvae seem to fit into this life history model. Larvae spawned in the Loop Current can be advected to the Gulf Stream off the southeastern U.S. where habitat is relatively unfavorable. Larvae just outside the Loop Current in the Gulf of Mexico retention areas could develop until they are mature enough to begin their migration to feeding areas along the middle and northern U.S. east coast.

The limited data on distribution of bluefin tuna young of-the-year support this hypothesis. Juvenile bluefin tuna appeared in diets of terns at the Dry Tortugas (24°30′N, 82°50′W) from early June to early July (Potthoff and Richards 1970). These juveniles ranged in length from 25 to 115 mm with all sizes present early in the season but only longer ones present later. No juvenile bluefin tuna were noted in April or May during eight years of observations although juveniles of other species of tuna were being eaten by terns during May. The juvenile bluefin tuna were apparently unavailable within the 24 km feeding range of the terns (Robertson 1964) until they began migrating through the Straits of Florida in June. The timing of the migration suggests that there is a distinct and discrete time for the young-of-the-year juveniles to migrate from their larval retention area to their juvenile habitat. Perhaps the larvae must develop enough to begin schooling just as herring do before they begin their migration. Migration by schools of newly transformed juveniles is consistent with the cohesive migration of other age classes of bluefin tuna (Brunenmeister 1980; Mather 1980). Larvae that were swept out of the Gulf in April and May would not be in synchrony with the migration of their year class in June and July unless they reached suitable retention areas off the southeastern U.S. There is no evidence for such areas. The larval retention areas thus play a dual role for bluefin tuna by supplying habitat for larval development and by affecting the timing of migrations of different life stages of the species. The larval retention areas we propose for bluefin tuna and other oceanic pelagic fishes differ from those of fixed size proposed for herring stocks because they are dynamic, varying in date of occurrence, geographical location, and area. This variability in the quantity of larval habitat is a density-independent environmental factor which may explain a significant amount of variability in recruitment of pelagic fishes. Variations in the quality of larval habitat (coincident prey and predators) would cause density-dependent effects within the constraints of the total larval retention habitat.

A quantitative knowledge of bluefin tuna larval retention areas will have two practical applications. The precision of larval surveys, which are the only current independent estimates of the spawning stock, may be improved by a stratified sampling design once the strata of low and high abundance can be defined. In addition, hypotheses about the importance of appropriate habitat for bluefin tuna and the effects on

recruitment of its temporal and spatial variability can be tested by comparing the fishery independent-variations in habitat with recruitment indices based on the catch statistics of commercial and recreational fisheries.

CONCLUSIONS

Larval bluefin tuna caught in the South Atlantic Bight in 1985 were in Gulf Stream water. Bluefin tuna larvae previously captured near Cape Hatteras were also in Gulf Stream water which meandered over the shelf edge. Larvae previously collected near Miami were primarily in the high velocity core of the Stream or in onshore meanders of the Stream. Therefore most bluefin tuna larvae off the southeastern U.S. were advected to the area, not spawned there. Although some unspent adults may spawn while migrating from the Gulf of Mexico to New England feeding grounds, only one of the larvae collected off the southeastern U.S. in 1985 had to have been spawned north of Miami based on its estimated age and rate of advection. The estimates of ages and advection do not falsify a hypothesis of local spawning with retention in recirculating currents, but the most likely conclusion considering all the evidence is that the South Atlantic Bight is not a major spawning area for western Atlantic bluefin tuna.

In addition, the habitat off the southeastern U.S. seems less favorable for bluefin tuna larvae because higher temperatures here than in the Gulf of Mexico would increase food requirements, and upwelling events over the shelf apparently do not lead to favorable food chains for larval tunas. Larvae may need to develop in retention areas outside the Loop Current in the Gulf of Mexico in order to synchronize their subsequent migration as schools of juveniles to nursery areas. These retention areas would be expected to vary in size and location with fluctuations in the Loop Current flow. The variations in amount of habitat for larvae could determine recruitment and thus affect the population dynamics of the bluefin tuna.

More research is needed to determine the survival rate of the larvae which are advected out of the Gulf of Mexico, to establish whether or not they recruit to the adult stock, to refine the definition of habitat for bluefin tuna larvae within the Gulf of Mexico, and to test if this habitat controls recruitment and population dynamics of the stock.

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Biomasses of Euphausiids and Smaller Zooplankton in the California Current—Geographic and Interannual Comparisons Relative to the Pacific Whiting, *Merluccius productus*, Fishery

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ABSTRACT: We examined data on size-fractionated zooplankton biomasses from the California Current in summer to 1) verify that euphausiid and smaller zooplankton biomasses varied in similar ways geographically and interannually, and 2) test for increase in euphausiid biomass after 1966, concurrent with initiation of a fishery on Pacific whiting (a major predator of euphausiids), and distinct from general, interannual changes. We accomplished purpose 1, but were unable to detect a significant effect attributable to the Pacific whiting fishery.

On the scale of years to decades and thousands of square kilometers, variability in the biomass of zooplankton, or of taxonomic categories within the zooplankton, can result from physical and chemical causes, from biotic interactions (especially in closed, manipulated systems such as lakes) or from some combination of these. In nonmanipulated systems, a plausible hypothesis is that variability results from a change in the physical processes influencing the area (the ultimate cause) plus ecological responses or readjustments of the populations present (the proximate cause). For the zooplankton of the open ocean, it is difficult to assess, by examination of case histories, the relative roles of physical and biological processes, because manipulation on the scales of interest is extremely difficult.

The California Current is known to vary interannually in transport and in physical properties—in aggregate, the Current's climate—the most extreme warming and decrease in southward flow being called El Niño (Wooster and Fluharty 1985). Correlated with (and in some sense probably caused by) these changes are variations in the biomass of zooplankton (Wickett 1967; Reid 1962). These changes are coherent through a large area—when zooplankton biomass is anomalously large or small in one area within the region, it tends to be large or small in all areas during the same year (Chelton et al. 1982). Further, several major taxonomic groups of zooplankton have similar interannual changes (Colebrook 1977).

By examining the timing of maximal zooplankton biomass relative to that of maximal southward flow, Roesler and Chelton (1987) concluded that off northern California interannual variations in biomass are caused by variations in direct advection of biomass from more northern regions (where biomass is high); off Baja California, variations in advection of nutrients from the north, translated via the food chain into zooplankton biomass with some lag, are more important.

Even in the presence of natural interannual variability, rapid development of a major commercial pelagic fishery is an anthropogenic manipulation which might cause detectable change in the biomass and/or composition of zooplankton. Pacific whiting, *Merluccius productus*, (also called Pacific hake) is one of the dominant fish in the California Current (Smith 1978). Euphausiids, especially *Euphausia pacifica* and *Thysanoessa spinifera*, make up > 70% of the weight of gut contents of whiting, especially fish <45 cm long, aged 3–4 years (Livingston 1983). *Euphausia pacifica* is a vertical migrator, at least much of the year (Brinton 1967; Brooks and Mullin 1983). *Thysanoessa spinifera* apparently remains in the upper 150 m at all times (Youngbluth 1976). Another prey of whiting, especially offshore, is the pelagic shrimp, *Sergestes similis*, (Alton and Nelson 1970), which has a nocturnal distribution similar to that of *E. pacifica* (Omori and Gluck 1979). Whiting guts are most full of food in the evening and early night (Livingston 1983), when the fish tend to be dispersed near the surface (Bailey et al. 1982).

In 1966 a foreign (later joint-venture) fishery, conducted from spring through fall, began removing considerable quantities of whiting in coastal regions off Washington, Oregon, and

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northern California (Nelson 1985). The commercial catch of pandalid shrimp in Oregon increased markedly at the time the Pacific whiting fishery began; from this coincidence, Bailey et al. (1982) and Francis (1983) suggested that the shrimp no longer eaten by whiting were available to fishermen, even though these commercial shrimp are only a minor portion of the whiting's diet. [Livingston and Bailey (1985) pointed out, however, that most of the increase in shrimp catch was due to increased fishing effort on shrimp rather than to increased catch per unit effort; hence it is not certain that the shrimp population has increased.] Nevertheless, the result and evidence of zooplanktivory summarized above stimulated an analogous question—whether the biomass of euphausiids increased in summer samples of zooplankton from the California Current off northern California in 1966–69, relative to summers of earlier years.

The trophic dynamics of the Pacific whiting, and the implications of the fishery, have been calculated from a simulation model by Francis (1983). His results indicated that the fishery may have reduced the (calculated) virgin whiting stock by about 21% without changing the annual production significantly because the production/biomass ratio increased. This conclusion implies that any indirect impact of the fishery on the whiting's food resources should be less than the change in the whiting's biomass. Francis also reasoned that the geographical distribution of food consumption by whiting would shift towards central California from northern California and Oregon.

Since the climate of the California Current is known to be correlated with interannual changes in the biomass of zooplankton, any change in euphausiid biomass must be scaled against the biomass of other zooplankton which would (presumably) be affected by climatic change but not directly affected by the removal of whiting. To test the assumption that the biomasses of euphausiids and smaller zooplankton respond similarly to climatic change, we reexamined data from the late 1950s, when there was a major El Niño.

We then determined the biomass of euphausiids and other pelagic shrimps (a major whiting food) relative to small zooplankton (not eaten by adult whiting) before and after the initiation of the fishery, and in a northern area closer to the fishery compared to further south, and then tested for significant differences. We also analyzed a published set of data from the California Current off cental Oregon (Pearcy 1976), since this was closer to the center of impact of the Pacific whiting fishery than were the samples available to us. Finally, we calculated whether, given the variances observed in the zooplankton samples we analyzed, we should have been able to detect a change in euphausiid biomass owing to partial removal of a major predator by the fishery.

METHODS

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) yielded samples of zooplankton from the California Current from the mid-1940s to the present. Though the CalCOFI net is not a perfect sampler of euphausiids and other large, active, pelagic shrimp, samples taken at night (when most of these species migrate into surface waters) do contain euphausiids. From 1951 through 1968, the standard net was of mixed silk mesh—a large, forward portion of 0.55 mm and a small, rear portion of 0.25 mm—towed from the surface to a depth of 140 m. In 1969, the standard was changed to a net of uniform 0.505 mm nylon mesh, towed to 210 m (target depth). Though these procedures have been intercalibrated (Smith 1974; Hewitt 1980), care in interpretation of differences between pre-1969 and 1969 samples is necessary.

We divided nocturnal, summer (June–October) CalCOFI samples into the following space/time blocks or categories (Fig. 1): North of Monterey (CalCOFI line 70), 1960–65—41 samples (24 inshore); south of Dana Point (CalCOFI line 90), 1960–65—172 samples (103 inshore); north of Monterey, 1966–69—47 samples (25 inshore); and south of Dana Point, 1966–69—116 samples (73 inshore). "Inshore" samples, treated as a separate subset because of the inshore nature of the whiting fishery, thus constituted 53–63% of the samples in each block. Twenty-one other samples, in which no euphausiids were found, were excluded from statistical tests; at least two such samples occurred in each space/time block. The samples were from the following CalCOFI cruises (designated "aabb", where aa = year and bb = month): 6007, 6010, 6107, 6110, 6210, 6407, 6507, 6509 (southern area only), 6606, 6607, 6608 (southern area only), 6610, 6907, 6908, and 6910. We made analogous divisions into space/time blocks in the CalCOFI data set from the late 1950s and the set from Oregon.

Each sample consisted of formalin-preserved, unsorted zooplankton captured at one station by

a nocturnal tow. We fractionated each sample by sieving a subsample (≤0.5 of the sample) through a 4 mm screen, and counted and manually placed the euphausiids (and sergestids) retained on this mesh on a preweighed glass fiber filter. We then rinsed all or part of the same subsample sequentially through 1 mm and 0.5 mm meshes, using recirculating seawater, and then rinsed the plankton passing 1 mm but retained by 0.5 mm onto another preweighed glass fiber filter. We then rinsed both filters and their catches with 6% ammonium formate, dried them overnight at 50°–60°C, cooled them in a desiccator, and reweighed them. Blank filters (no zooplankton) were treated similarly. The dry weight of the sample, corrected for initial filter weight and any weight change of the blank filters, times the subsampling factor and divided by the volume of water filtered by the original net tow, is the biomass of "euphausiids" or of "small zooplankton" (that retained by the 0.5 mm mesh) for that station, and the weight of the euphausiids divided by their number is the dry weight per euphausiid.

With particular regard to the Pacific whiting fishery, which started in 1966 in the northern part of the California Current, and the expectation that biomass of whiting food might increase, we tested the following null hypotheses (stated in the "one-tailed" forms appropriate for our expectations).

H_{01}—Absolute biomass of euphausiids in the northern area was not greater from 1966 onward than that before 1966.

H_{02}—The ratio of biomasses (euphausiids/small zooplankton) in the northern area from 1966 onwards was not greater than a) this ratio before 1966, or b) that in the southern area. [The small zooplankton biomass is used to correct for the expected north-to-south differences, overall changes in the biomass of zooplankton, or change in sampling techniques, throughout the California Current for reasons other than the whiting fishery.]

H_{03}—The dry weight per euphausiid in the northern area was not greater from 1966 onward than before 1966.

Hypothesis H_{02}a, for example, was examined by a one-tailed rank sum (Mann-Whitney U) test of whether the median of all ratios at northern stations before 1966 was statistically indistinguishable from the median for all such stations beginning in 1966. The alternative which would be consistent with an effect of the whiting fishery would be, pre-1966 median <1966-and-later median. In some cases, analogous *t*-tests were also performed on data normalized by log-transformation to determine whether transformed means differed. In this approach, all stations within one block of geography and time are treated as equally valid estimates of the overall median, independent of location of the stations within the block.

There are significant inshore/offshore gradients in biomass (see below), and comparisons between years or between areas could be confounded by differences between groups being compared in the inshore/offshore locations of usable samples. We took several precautions to prevent this; first, we tested for such gradients in our own samples by comparing medians from inshore and offshore subsets of stations by rank sum tests. We also tested hypotheses H_{01}–H_{03} using only the inshore subsets of the stations (Fig. 1); this was done partly because the fishery for whiting is generally conducted in areas shallower than 500 m.

We tested analogously data from a transect off Oregon which was repeatedly sampled from 1962 to 1967 (see below).

Hypotheses H_{01} and H_{02}a were tested further by another approach which acknowledges that within each major space/time block, stations may differ systematically because of geography (e.g., an inshore/offshore gradient), so that the identity of each station should be retained in the test. The data from each northern California station which was sampled at least thrice before 1966 or in 1966–69, and at least once during the contrasting period, were ranked separately as for a rank sum test, but the summed ranks were then combined for testing against the expectation from the null hypotheses. There were 7 stations used in this test, and 21 data points from each period.

Falsification of these hypotheses implies that there was a significant increase in euphausiid biomass (and/or individual size) coincident with the whiting fishery and that this increase was unlikely to be caused by other factors affecting zooplankton in the whole California Current, including those types on which adult whiting do not feed.

In order to validate the assumption which underlies H_{02}—that small zooplankton and euphausiid biomasses vary in parallel in response to the California Current's climate—we

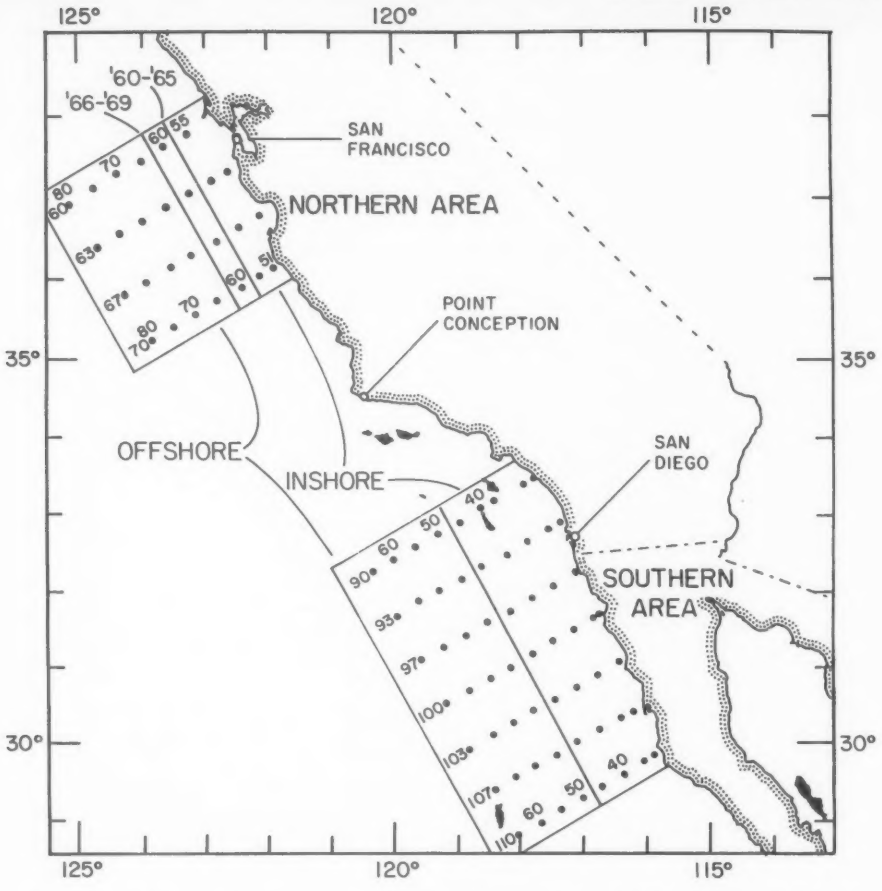

FIGURE 1.—Northern and southern areas, and CalCOFI transect line and station numbers. Each area is divided into "inshore" and "offshore" subsets of stations: the dividing line used in the northern area for 1960–65 was closer to shore than that for 1966–69 because the distribution of samples differed. The same areas were used for data from the 1950s, with same inshore/offshore divisions as in 1960–65.

used published data from 1958 and 1959, during which there was a major El Niño, compared with 1955–57. Zooplankton from the California Current during these years had been visually classified into 17 categories, and wet weight biomasses were assigned to each (Isaacs et al. 1969). We examined "euphausiid" and "copepod" categories of this data set (assuming from our visual examination that the "copepods" were most similar to our "small zooplankton" category), selecting those stations which were nocturnal and within the areas defined in Figure 1 during April, July, and October, and separating 1955–57 from 1958–59. This resulted in 21 northern, 1955–57 stations (13 of which were inshore); 49 northern, 1958–59 stations (30 inshore); 118 southern, 1955–57 stations (72 inshore); and 110 southern, 1958–59 stations (63 inshore). We then performed statistical tests analogous to those described above to test hypotheses concerning similarity of geographic and temporal variation of euphausiid and copepod biomasses, and constancy of their ratio.

RESULTS

Interannual Variation of Euphausiids and Copepods, 1955–59

Colebrook (1977) demonstrated by multivariate analysis overall north-to-south and inshore-to-offshore trends in the annual mean values of zooplankton biomass in the California Current. He found that the biomasses of euphausiids and

copepods particularly decreased moving offshore. The biomasses of both categories were larger in 1955 and 1956 (pre-El Niño years) than in 1958 and 1959 (El Niño years; see also Chelton et al. 1982). This suggests that biomasses of euphausiids and of the smaller copepods respond similarly to interannual climatic or environmental variation.

Our results, which are summarized in Figure 2, were

1) Biomasses of euphausiids and copepods were significantly less in the southern area than in the northern area, both before (1955–57) and during (1958–59) the El Niño, in agreement with Colebrook's (1977) conclusions, and the ratio of euphausiid to copepod biomasses did not change significantly. Analysis of data from only the inshore subareas yielded the same results, except that the euphausiid biomass did not differ significantly between northern and southern inshore areas during 1958–59.
2) Biomasses of euphausiids and copepods were significantly less during El Niño than before it, both in the complete areas and in the inshore portions (also agreeing with Colebrook's result), and the euphausiid/copepod biomass ratio did not change significantly.
3) Neither the euphausiid nor the copepod biomasses were significantly different between inshore and offshore subareas, nor were the ratios significantly different (comparison not shown in Figure 2); this result differs from Colebrook's conclusion.

Overall, we conclude that it is reasonable to use the biomass of small zooplankton to correct or scale the biomass of euphausiids for effects of geography or interannual climatic variation in order to test for changes due to factors specific to the euphausiids.

Interannual Variation in 1960–69 off California

Averaged over the entire decade, there were significantly lower biomasses of euphausiids and of small zooplankton offshore than inshore, both in the southern area by itself and in the combined areas (unlike our result for 1955–59). Thus, for testing hypotheses (such as H_{01}) concerning biomasses, the inshore/offshore distribution of samples should be similar in the sets being compared (as was true in our case). We were unable, however, to reject the null hypothesis that the median ratio of biomasses in the offshore subset of stations equalled the median

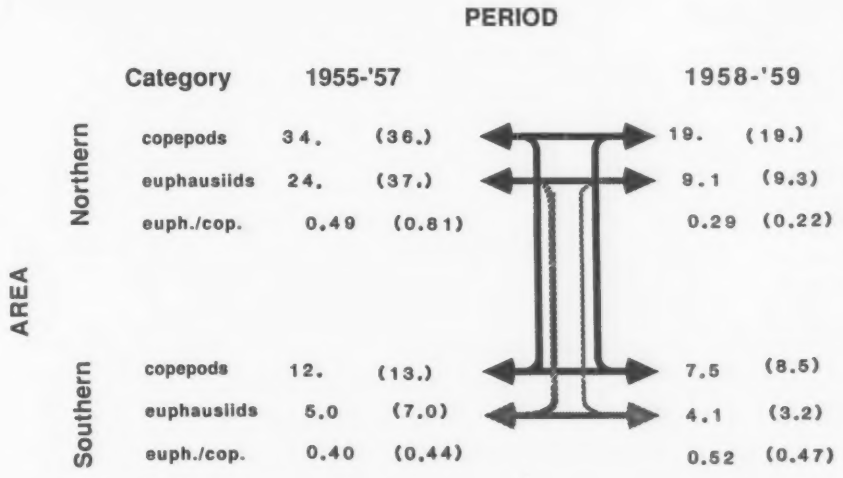

FIGURE 2.—Overall and (inshore subset) medians for each space/time block in the 1950s, for wet weight biomasses ($mg \cdot m^{-3}$) of copepods and euphausiids, and for the ratios at individual stations. Arrows connect medians which differed significantly ($P < 0.05$ for H_0 = no difference); a thick arrow indicates that the comparable medians of the inshore subsets of data also differed significantly. All comparisons were "vertical" or "horizontal"; no "oblique" comparisons were tested (e.g., no comparison between northern, 1960–65, and southern, 1966–69).

ratio at the inshore stations, either in the northern and southern areas separately or in the combined areas. Since we could not detect persistent gradients by this test (nor by analogous *t*-tests), we concluded that differences in the inshore/offshore placement of samples between two groups should not preclude the testing of hypothesis H_{02}, which concerns ratios.

In comparisons between periods or between areas (Fig. 3), the most significant difference was the greater biomass of the "small zooplankton" in the north in 1966–69 than the northern, 1960–65 or the southern, 1966–69 biomasses. These differences were significant ($P < 0.05$) even when the inshore subsets of data only were considered. Probably as a result of this, the ratio of euphausiid to small zooplankton biomasses was significantly lower in the northern, 1966–69 data set than elsewhere. This difference was also significant by *t*-test.

The biomass of small zooplankton was significantly greater in the northern than in the southern area in both periods, in fact (as in 1955–59). The null hypothesis that the biomass of euphausiids was the same in all sets of data could not be rejected. Nor did the weight per euphausiid in the northern area change.

These results were supported by the comparison of biomasses at specific northern stations which had been sampled several times. The biomass of small zooplankton was greater, and the euphausiid/small zooplankton ratio less, in 1966–69 than in 1960–65 ($0.05 < P < 0.1$ by two-tailed test in both cases), while the biomasses of euphausiids did not differ ($P > 0.1$).

The significant increase in median biomass of small zooplankton in 1966–69, relative to 1960–65, could have been due to the inclusion of data from 1969, when samples were taken differently (see Methods) if the different method itself resulted in increased catch. However, Smith (1974) reported that the method used in 1969 resulted in a *smaller* biomass (per unit volume filtered) than did the pre-1969 method. In our data, the biomass of small zooplankton was greater, and the euphausiid/small zooplankton ratio less, in 1966 than in 1969 (rank sum tests). Hence, the change in sampling in 1969 could hardly have been responsible, in itself, for the elevated biomass of small zooplankton in 1966–69 relative to the earlier years.

Thus, euphausiid biomass could not be shown to increase coincident with the onset of the whiting fishery, either in absolute units or relative to the small zooplankton. None of the null hypotheses relating to absence of change of euphausiids in the northern area at the time of the whiting fishery could be rejected, and in fact the ratio of

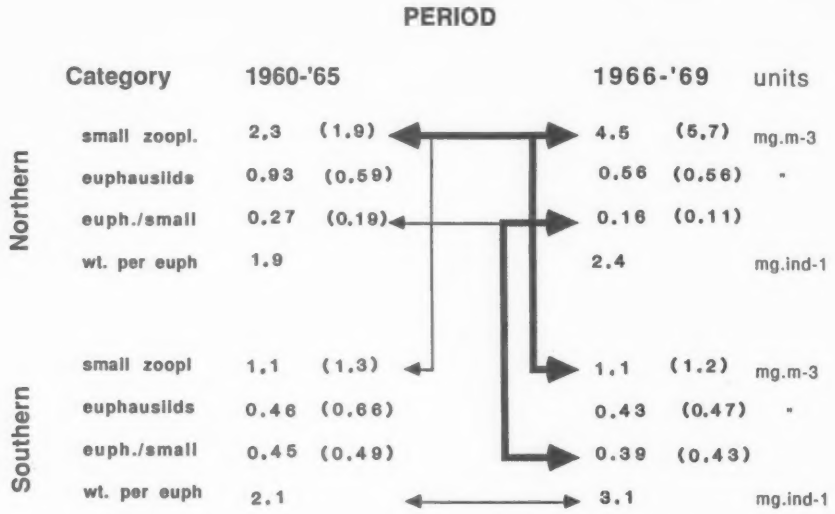

FIGURE 3.—Overall and (inshore subset) medians for each space/time block in the 1960s, for dry weight biomasses of small zooplankton and euphausiids, their ratios, and the dry weights per euphausiid. Arrows connect medians which differed significantly ($P < 0.05$ for H_0 = no difference); a thick arrow indicates that the comparable medians of the inshore subsets of data also differed significantly. All comparisons were "vertical" or "horizontal"; no "oblique" comparisons were tested.

euphausiid to small zooplankton biomass differed significantly in the direction opposite to that predicted.

Interannual Variation in 1962–67 off Oregon

We also examined similar hypotheses using data provided by W. G. Pearcy (see Pearcy 1976) for a repeatedly sampled transect from the Oregon coast seaward to 530 km, since this region is closer to the geographic center of the Pacific whiting fishery than was our California, northern area. The data set includes 89 values for dry weight biomasses of euphausiids and copepods from nocturnal samples from April to October 1962–67. By analogy to our treatment of California data, we defined inshore as the innermost 100 km, and offshore as the remainder of the transect; we therefore divided this set into subsets, 1962–65 (56 total samples, 34 inshore) and 1966–67 (33 samples, 20 inshore).

To compare results from this Oregon transect to one transect within the "southern" area, we chose CalCOFI line 93 (see Figure 1), and subdivided samples from it into similar subsets: 1960–65 (33 samples, 17 inshore) and 1966–69 (23 samples, 14 inshore). The direct comparison of biomass off Oregon to that on line 93 means little, since the methods differed (for instance, we measured "small zooplankton" and Pearcy measured copepods), but we could compare the patterns of variation shown on the two transects.

On line 93, biomass of euphausiids was significantly less offshore than inshore (as was true for the entire southern area), and the biomass of small zooplankton tended similarly, though the difference was nonsignificant. Neither the small zooplankton nor the euphausiid biomass, nor their ratio, differed between 1960–65 and 1966–69—conclusions which also characterized the entire southern area (Fig. 3). The Oregon transect revealed a similar spatial pattern (significant decreases of biomass offshore for both copepods and euphausiids) and a similar lack of temporal change (no significant changes for the entire transect, or its inshore portion, in copepod biomass, euphausiid biomass, or their ratio) between 1962–65 and 1966–67.

Therefore, the patterns off Oregon were very similar to those off southern California, and failed to indicate a change in the biomass of euphausiids concurrent with the whiting fishery off Oregon.

Expected Response of Euphausiid Biomass to the Pacific Whiting Fishery

Detection of a change in the biomass of euphausiids which could be caused by the start of the whiting fishery depends on 1) the magnitude of the change in the predatory impact on euphausiids due to change in the stock of whiting, 2) the rapidity with which the community readjusts to such changes, and 3) the variability among the available samples in which change is to be detected. Francis (1983) calculated the food consumption by the virgin and exploited whiting stocks in several standard regions of the North American west coast; these estimates can be applied to the areas we sampled by making various assumptions about the more detailed geography of the effect of the fishery on the whiting stock. The variances of the groups of samples we analyzed give an estimate of the "noise" against which this "signal" must be detected, and, as discussed above, we can use the biomasses of copepods to correct for long-term variability.

Since we were unable to detect a change in biomass of euphausiids attributable to the Pacific whiting fishery, we did a simple calculation to determine how many samples, with the same variances as the samples we did analyze, we would have had to analyze to detect an expected change at the 0.05 probability level, if 1) only the change in whiting stock affected the biomass of euphausiids, or 2) if changes in the biomass of small zooplankton were used to normalize the euphausiid biomass for nonfishery effects (i.e., using a simplified euphausiid/small zooplankton biomass ratio).

First, we assumed that the biomass of euphausiids was in equilibrium before the start of the fishery in 1966, such that the sum of mortality and growth was zero and immigration equalled emigration, and that subsequently a biomass of euphausiids simply accumulated, proportional to the decrease in whiting predation, without change of the population parameters. We averaged the biomasses of euphausiids from all samples in a given area from 1960 to 1965, and then calculated the expected biomass two years after the start of the fishery from the change in consumption by whiting in that area, using the estimates of Francis (1983) corrected for the fraction contributed by euphausiids to whiting gut contents (Alton and Nelson 1970; Livingston 1983; Rexstad and Pikitch 1986), for the dry/wet weight ratio, and for the volume represented by

that area. Thus, we calculated an "expected" biomass of euphausiids at the end of 1967, E_a, from the mean biomass before the start of the fishery, E_b. The maximum expected increase was 50% in the northern California inshore area.

To test for significant differences by two-sample t-test between the means of nonnormal data sets, we would transform to logarithms and verify that this normalized the data (as was true for our data sets) before performing the test. If the means of the log-transformed data are E_a^* and E_b^*, the critical value for the t-test, for given numbers of samples, then indicates how much E_a^* must exceed E_b^* for the difference to be significant, given the variance around E_a^* and E_b^*, and thus defines a critical ratio, $(E_a/E_b)_{cr}$, for nontransformed data (see Appendix A). Conversely, we can ask how many samples would need to be analyzed from a particular area such that $E_a/E_b > (E_a/E_b)_{cr}$.

We did this calculation for the entire areas, and the inshore portions, of northern California and Oregon. In order to detect significance, we would have had to analyze between 80 and 1,600 samples for each block of time within an area, depending on the area. Therefore, the numbers of samples we analyzed, and the data set from Oregon, were insufficient to detect the simplest expectation.

Next, to normalize the euphausiid biomasses, we multiplied the ratio, E_a/E_b, by the comparable ratio of means of observed, log-transformed, small zooplankton or copepod biomasses to obtain a ratio of euphausiid biomasses, $(E_a/E_b)_{corr}$, corrected for the environmental or climatic change reflected in these biomasses, which increased significantly off northern California (Fig. 3), and compared $(E_a/E_b)_{corr}$ to $(E_a/E_b)_{cr}$. In the Oregon data set, $(E_a/E_b)_{corr} < (E_a/E_b)_{cr}$, the expected change could not have been detected with the available data. In both inshore and total areas of northern California, however, $(E_a/E_b)_{corr} > (E_a/E_b)_{cr}$ meaning that a t-test should have been able to detect a significant increase in biomasses of euphausiids in northern California due to the combined effect of environmental change and the whiting fishery, if only these two factors operated in the most simple, additive fashion.

DISCUSSION

Our results, like those of Colebrook (1977), show considerable similarity in the large-scale geographic and interannual variations in biomass of euphausiids (at least those caught by the CalCOFI net at night) and smaller zooplankton. It is also clear that the impact of a climatic event like El Niño greatly exceeds, on these scales, any effect of the whiting fishery.

The failure to find greater biomasses of whiting prey after the beginning of the fishery in the Californian area north of Monterey, or off central Oregon, could result from undersampling, from a mismatch between the effect of the fishery on the whiting population and the zooplankton sampled by plankton nets, and/or from the complexity of the ecological relations affecting euphausiid biomass.

"Undersampling" means that variability within each space/time group of samples is so great that we cannot statistically detect differences between groups even though differences actually exist which would be detected if more samples were available. As we have shown, the change in euphausiid biomass calculated from a model of the biomass and food consumption of exploited and virgin Pacific whiting stocks could not have been detected statistically without at least three times the number of samples we had. Further, the actual biomasses of euphausiids off both northern California and Oregon tended to decrease, as did the ratios of euphausiid to small zooplankton (or copepod) biomasses. Therefore, we doubt that simply analyzing more samples of the same kind (i.e., from the same sampling pattern, using the same gear) would demonstrate the anticipated increase in the biomass of euphausiids.

Because CalCOFI stations north of San Francisco were not sampled after April of 1960 during that decade and because the whiting fishery was centered off Oregon and Washington, the samples in our northern California area (Fig. 1) were too far south to be ideal for this analysis, as well as extending too far offshore. The transect off Oregon was better placed latitudinally, but the number of samples in the inshore zone (where the Pacific whiting fishery was conducted) was rather small. Therefore, our effort to increase the number of samples to be analyzed resulted in inclusion of areas outside that where the predators had been reduced by the fishery; we were, in a sense, trying to detect advection or diffusion of the effect into a larger area.

Ecological complexity may have buffered the response to a reduction of a predator such as whiting in ways that do not ameliorate climatic effects. The relatively simple outcome—that euphausiids became absolutely or relatively

more abundant following the initiation of the fishery—could have been overshadowed by, e.g., 1) replacement of whiting by the increase of some other species of predator on euphausiids, even a species which is also prey for large whiting (Livingston 1983); 2) differential removal of large whiting by the fishery, leaving smaller whiting whose preference for euphausiids as food exceeded that of the larger fish, so that predation pressure did not decrease dramatically because of altered age structure of the whiting population; or 3) replacement of predator-limitation by food-limitation of euphausiid biomass.

We tried to minimize the effect of response 1) by restricting the post-1965 analysis to the years immediately following the initiation of the fishery, on the theory that this might have represented a period of abundant euphausiids before the ecosystem returned to a new equilibrium through the increase of a new, major zooplanktivore. Unfortunately CalCOFI coverage of the northern California Current in the summers of 1967 and 1968 was very small.

Response 3) is possible (indeed, euphausiid biomass may never have been limited by Pacific whiting's predation), but the increase in biomass of small zooplankton in the northern California area in 1966–69 (Fig. 3) suggests a food supply which could have supported an increased biomass of euphausiids—an increase which was not realized.

In considering the possible responses of the zooplanktonic community to the Pacific whiting fishery, it is worth remembering that there have been natural fluctuations in the whiting population as great as those caused by fishing. Oceanographic variation in the whiting's spawning area is important, higher temperatures being associated with greater, and more variable, recruitment (Swartzman et al. 1983; Bailey and Francis 1985). Judging from scales collected in an anoxic basin, whiting was much more abundant off Southern California in the 30 years around 1900 than in recent years (Soutar and Isaacs 1974). Such fluctuations in the stock of whiting are therefore only a manifestation or symptom of more general environmental variation in the California Current.

Overall, our results indicate that a major environmental perturbation, such as El Niño, acts on the California Current's ecosystem as a whole (though the mechanism of action may differ geographically; Roesler and Chelton 1987) and modifies the components we studied in similar ways. The system seems to adjust to more local, specific modifications, such as anthropogenic changes in biomass and age structure of one predator, so that widespread effects on planktonic prey populations are difficult to detect.

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APPENDIX A

Caution must be used when performing a logarithmic (ln) transformation [$y_i = \ln(x_i)$] on data (x_i) belonging to a nonnormal distribution. The resulting mean of the log-transformed data

$$\bar{y} = \frac{\sum_{i=1}^{n} \ln(x_i)}{n}$$

is equal to the logarithm of the geometric mean of the untransformed data

$$\bar{y} = \ln\left(\sqrt[n]{\prod_{i=1}^{n} x_i}\right).$$

Since the geometric mean is always less than the arithmetic mean (Zar 1984), the antilog of the mean of the log-transformed data must be corrected before it can be used as an unbiased estimation of the arithmetic mean of the untransformed data.

Bagenal (1955) showed a relationship between the means of transformed ($\bar{y}$) and untransformed ($\bar{x}$) data, which is valid when the transformed data belong to a normal distribution, with mean = $\bar{y}$ and variance = σ_y^2.

$$\bar{x} = e^{\bar{y} + \frac{1}{2}\sigma_y^2} \tag{1}$$

and

$$\bar{y} = \ln(\bar{x}) - \frac{1}{2}\sigma_y^2 \tag{2}$$

We applied this relation to our calculations of the critical differences between the means of log-transformed biomasses after and before the beginning of the fishery. The data had to be log-transformed in order to perform the two-sample t-test, since this assumes that the distributions underlying the two samples are normal.

The critical differences were so calculated, from the two-sample t-test formula:

$$E_a^* - E_b^* = t!\, s_p \sqrt{\frac{n_a + n_b}{n_a\, n_b}} \tag{3}$$

where E_a^*, E_b^* are, respectively, the means of the log-transformed biomasses after and before the beginning of the fishery, equal to $\bar{y}$ in Equation (2),
$t!$ is the critical t-value at $\alpha = 0.05$,
s_p is the pooled variance for the two samples, and
n_a,n_b are, respectively, the numbers of samples after and before the beginning of the fishery.

These differences were then related to the means of untransformed data by applying Equation (2):

$$E_a^* - E_b^* = \ln(E_a) - 0.5\, s_p^2 - \ln(E_b) + 0.5\, s_p^2 = \ln\left(\frac{E_a}{E_b}\right) \tag{4}$$

where $E_{a,b}$ indicate arithmetic mean of untransformed biomasses, analogous to $\bar{x}$ in Equation (1).

And therefore, from Equations (3) and (4), a critical ratio was defined:

$$\left(\frac{E_a}{E_b}\right) \text{cr} = e^{\left(t' s_p \sqrt{\frac{n_a + n_b}{n_a n_b}}\right)} \tag{5}$$

which is the minimum ratio necessary to reject the null hypothesis.

Note, however, that the correcting factors ($0.5\ s_p^2$) cancel each other only when using a t-test with pooled s^2, i.e., when assuming the two samples belong to the same distribution.

Growth During the Larval and Juvenile Stages of the Northern Anchovy, *Engraulis mordax*, in the California Current During 1980–84

John L. Butler

ABSTRACT: Increment widths and back-calculated growth rates for northern anchovy, *Engraulis mordax*, did not differ during the years 1980–84. This evidence of stable larval growth rates does not support the theory that it is the variation in larval growth rates that directly affects the magnitude of recruitment. Furthermore, since growth rates remained stable, even though zooplankton volumes in 1983 were well below the long-term mean, it follows that surviving post-first-feeding larval anchovies may not be food limited.

The size of juvenile northern anchovy was reduced during the 1982–83 El Niño "phenomenon" in the California Current. Mean lengths of anchovy juveniles collected in the fall were greatest in 1980, least in 1982, and intermediate in 1981, 1982, and 1984. Growth rates back calculated from otolith increment widths did not differ significantly between the 1980 and 1983 cohort, until 100 days after first feeding. Reduced growth after 100 days largely determined the smaller size of 1983 anchovy juveniles. Condition factor was also reduced in the 1983 cohort. The 1982 cohort was not greatly affected, because El Niño did not have a pronounced effect off the North American coast until well after the 1982 northern anchovy spawning season.

Through the years, the overall abundance of many pelagic fishes varies with the strength of individual year class; changes in mortality rates early in life (Hjort 1914, 1926), rather than parent stock size, may determine the size of individual year classes. Considerable controversy, however, surrounds details of the exact stage and mechanism through which changes in individual year-class strength occur.

The co-occurrence of fish larvae and their food is a mechanism that has been proposed to explain variations in year-class strength (Hjort 1914, 1926). Lasker (1978) has shown that food availability may affect survival of first-feeding northern anchovy, *Engraulis mordax*, larvae in the sea. Food availability may not affect the survival beyond the first-feeding stage; however, Methot (1981) found that early larval anchovy growth rates in the sea were the same as those of well-fed, laboratory-reared larvae. Survival through the larval stage does not determine the magnitude of the northern anchovy recruitment (Peterman and Bradford 1986; Peterman et al. 1988). Thus food availability for larvae may not determine the year-class strength and whether food availability affects juvenile survival are yet to be investigated.

A simulation model of the northern anchovy population indicates that the growth rate of late larvae and early juveniles may affect the magnitude of recruitment (Smith 1985). If mortality rates in the marine environment are size-specific, as predicted by Peterson and Wroblewski (1984), and if growth rates determine the duration of the most vulnerable stages, reduced growth should adversely affect survival. The extent to which growth rates of late larvae and juveniles vary is unknown.

The growth rate of juveniles also affects adult size. Off southern Baja California, the adult size of northern anchovy is entirely determined by juvenile growth, because these fish show no growth after 18 months (Parrish et al. 1985). Analysis of the regional patterns of growth of northern anchovy shows that the average length of fish at a given age increases from south to north. The length at 18 months ranges from 101.1 mm off southern Baja California to 126.6 mm off central California (Parrish et al. 1985).

Because batch fecundity is a function of body size in broadcast spawners, the juvenile and adult growth rates determine the reproductive capacity over the adult lifespan. Competition among juveniles for resources affects adult fertility in other species (Prout and McChesney 1985), and, if growth of juvenile pelagic fishes is food limited, competition among juveniles may

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be a mechanism of density-dependent compensation.

Growth rates of larval and juvenile anchovy during El Niño periods are of particular interest, because the growth rates during an environmental perturbation may reveal details of the processes of growth and survival during normal conditions. During the 1982–83 El Niño event off California, temperatures were elevated (Lynn 1983; Simpson 1983) and zooplankton density was reduced in 1983 (McGowan 1985). If planktivorous fish compete for food, competition should be highest when zooplankton abundance is lowest. Comparison of growth rates throughout the larval and juvenile stages during periods of low and high food abundance may show the size range at which the larval or the juvenile stage is most important. In this paper I examine the interannual variability in growth rates of anchovy larvae and juveniles during periods of low and high food abundance.

METHODS

Samples of juveniles from the central population of northern anchovy were obtained from midwater trawl hauls taken in 1980–84 by the Sea Survey Program of the California Department of Fish and Game. Annual cruises to monitor the strength of the incoming year class of northern anchovy have been conducted during September and October since 1976; Mais (1974) has described the gear and sampling procedures. The surveys extended along the Pacific coast from central Baja California to Point Conception, CA, with the exception of 1982, when the southern limit was the U.S.-Mexican border. Trawl hauls were taken nearshore inside of a 75 fm contour where young of the year are most abundant during the fall (Parrish et al. 1985).

Twenty five juvenile northern anchovy were randomly taken from each positive trawl haul and frozen for age determination. A subsample of 200 juvenile anchovy was randomly taken from the 800 to 1,000 fish collected on each survey for analysis of growth rate using daily increments in the otoliths. Fish were measured from the tip of the snout to the posterior edge of the hypural plate (standard length), and otoliths were removed and mounted on microscope slides using Eukitt[1] mounting medium.

Growth rates and ages of juvenile northern anchovy were determined by counting and measuring daily increments in the otoliths (Methot 1981). The increment widths were measured and recorded along a transect from the focus to the posterior margin of the otolith (otolith radius), using a video-coordinate digitizer connected to a microcomputer. The otoliths were progressively polished between readings, using 15 and 0.3 μ lapping film, to reveal increments along the entire transect. Data from different areas of the otolith were collected as the increments became visible. During each reading groups of 10 or less (typically five) increments were counted and measured. The number of increments measured was reduced if width varied among increments.

ANALYSIS AND RESULTS

Data from both otoliths and several replicate transects per otolith were combined to calculate age and otolith increment widths (Methot 1981). Mean increment width was calculated at each point along the radius from the focus to the posterior margin of the otolith. In some cases, it was impossible to obtain measurements of all increment widths in the otoliths. In these cases, increment widths were interpolated using linear approximation (see Methot 1983 for details). Data for increment widths and age estimates were not used if more than 5% of age was calculated from interpolated increments.

A direct comparison of the average size of recruits from year to year is inappropriate because their ages may differ from year to year owing to differences in the dates of spawning (Methot 1983) or to dates of collection. To eliminate this bias, the dates of hatching were determined from the dates of sampling and ages, and fish were grouped by year and month of hatching.

Interannual and seasonal differences in length were tested, using an analysis of covariance (Bartlett et al. 1984) with age as the covariate. This analysis adjusted the mean length to the grand mean age of 208 days, approximately the time elapsed from the peak of spawning to the date of capture. Since the relation of length to age is typically nonlinear, some error is introduced using a linear adjustment. The difference in dates of sampling is, however, only about one month and the relation of size to age is approximately linear from two to six months.

Analysis of covariance of these data indicates parallel lines with differences in means (Case 2c

[1]Reference to tradenames does not imply endorsement by the National Marine Fisheries Service, NOAA.

in Bartlett et al. 1984). Thus, comparison of lengths adjusted by age between years of fish hatched during the same calendar month is reliable. Comparison of lengths of fish hatched at the extremes of the same spawning season may be less reliable than between-year comparisons. Fish hatched in January are four months older than fish hatched in May, and linear extrapolation to a common age may introduce error. However, since growth is decelerating, linear extrapolation overestimates mean lengths of fish hatched at the extremes of the spawning season. The fact that lengths of fish hatched in January and May in all years, except 1983, are less than lengths of fish hatched in March indicates that the error is not great.

The allometric relations of length and weight to otolith radius were estimated using nonlinear regression. These relations were used to back-calculate age-specific size and growth rates for individual fish; not all fish were weighed in 1980 and 1981, and data were pooled from 1980 to 1982 to determine the allometric relations of both length and weight to otolith radius. Individual relations were determined for 1983 and 1984.

The growth rates in length and in weight were determined from increment widths and the first derivative of the empirical relationship of fish size and otolith radius. The condition factor (dry weight/length cubed) was significantly less in anchovy juveniles collected in 1983 than in anchovy juveniles collected in 1980–82. Therefore, the algorithm to convert otolith increment size to growth in dry weight differed among years. The equation used to calculate growth in length was

$$\Delta L/\Delta t = (\Delta R/\Delta t)(\Delta L/\Delta R); \qquad (1)$$

where $\Delta R/\Delta t$ is rate of change of the width of the daily increments, and $\Delta L/\Delta R$ is the slope of the observed relationship of fish length and otolith radius.

The variance of the product (Y) of two variables (X, Z) is given by

$$\mathrm{Var}(Y) = Z^2\mathrm{Var}(X) + X^2\mathrm{Var}(Z) + 2XZ\,\mathrm{Covar}(XZ) \qquad (2)$$

if the variables are not independent (Goodman 1960). The estimate of the variance of $\Delta R/\Delta t$ was the variance of the measurement of increment width of the fish in each group. If the length, radius relation was linear, the variance of $\Delta L/\Delta R$ was estimated from $S^2_{Y|X}$, the variance of the slope of the regression of length on otolith radius. If the relation of length to radius was nonlinear, as was often the case, the variance of $\Delta L/\Delta R$ was estimated by partial derivatives. The variance of $\Delta W/\Delta R$ was not calculated; the complex derivative may not be a good estimate of the true variance.

The author tested the assumption that the covariance was equal to zero by comparing the slopes of the relations of juvenile fish length and otolith radius for 70–100 mm, slow- and fast-growing fish collected in October 1984 that were ≥ 1 year old. The slope was 0.0419 for anchovy older than one year and 0.0314 for fish younger than one year old. These slopes were not significantly different ($P > 0.10$, ANCOVA). Consequently confidence intervals around back-calculated growth rates were calculated ignoring the third term in Equation (1).

Lengths of anchovies were significantly different between months and years ($P < 0.01$, ANCOVA). Within a spawning season, fish hatched during February, March, and April grew faster than fish hatched in January or May (Fig. 1), although this was not evident for the 1983 or 1984 data. The mean of five fish in January 1982 was not different from that of the April 1982 sample. The adjusted lengths of juveniles collected from the 1983 year class where less than the adjusted lengths of any of those from 1980–82 for all months but May (Fig. 1, Table 1). The adjusted lengths of juveniles from

TABLE 1.—Mean lengths at capture of juvenile northern anchovy hatched in various months of 1980–84, adjusted to a common age of 208 days. SE and *N* stand for standard error and number of fish, respectively.

	Month of Hatching				
Year	Jan.	Feb.	Mar.	Apr.	May
1980	71.4	78.7	84.6	83.6	72.3
SE	3.6	1.6	1.0	1.6	
N	7	30	104	33	2
1981	77.0	79.9	83.5	82.7	79.7
SE	2.2	2.2	1.2	1.5	2.4
N	21	29	42	35	16
1982	81.1	85.79	84.1	81.0	78.9
SE	4.5	1.3	1.1	1.2	1.6
N	2	32	70	53	29
1983	70.0	71.4	71.5	70.8	73.7
SE	2.6	2.1	0.9	0.9	2.7
N	9	17	99	45	8
1984	74.8	77.0	76.0	76.8	75.6
SE	1.5	1.3	1.3	1.9	1.5
N	39	53	42	22	17

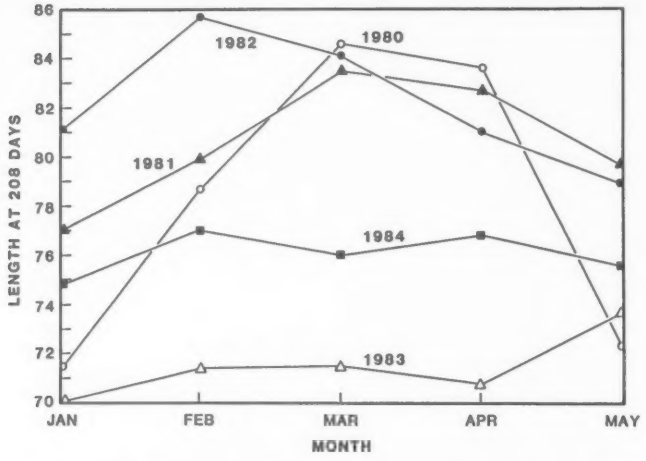

FIGURE 1.—Mean lengths adjusted for age of northern anchovy spawned in 1980–84. For each year, fish are grouped by back-calculated date of hatching, and length at capture is adjusted to mean age of 208 days.

1984 were intermediate between those of 1980–82 and 1983.

Fish hatched during 1983 did not grow more slowly throughout the entire larval and juvenile stage than during other years. Otolith increment widths from 104 juveniles hatched in March 1980 were compared with otolith increment widths from 99 juveniles hatched in March 1983 (Fig. 2). In fish smaller than 40 mm in length, increment width was not different. Above 40 mm, the otolith increment widths were smaller in the 1983 sample than in the 1980 sample ($P < 0.01$); the 95% confidence limits for the two cohorts did not overlap. These results show that the difference in lengths of the two cohorts indicated by the analysis of covariance is largely due to difference in growth rate after a size of 40 mm, rather than to a reduction of growth throughout life.

Back-calculated lengths and growth rates of 1980 northern anchovy juveniles were greater

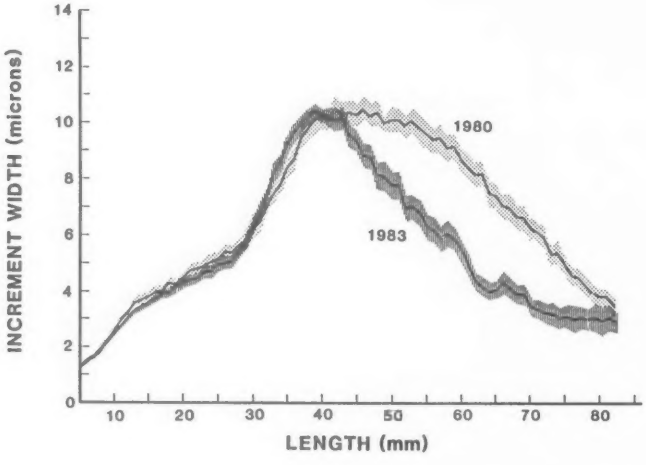

FIGURE 2.—Average otolith increment width versus length of 104 northern anchovy spawned in March 1980 and of 99 anchovy spawned in March 1983. Shaded areas are 95% confidence intervals.

than those of 1983 (Figs. 3, 4). Cohorts did not differ significantly in growth until approximately 40 mm. The age of the end of the late larval (10 mm) period was 20 days in 1980 and 19 days in 1983. A local minimum for growth rates of 1983 fish occurred at about 35 mm and at about 42 mm for growth rates of 1980 fish. This corresponds, approximately, to metamorphosis from late larval stage to juvenile stage. The duration of the late larval period (10–35 mm) was about 70 days in both 1980 and 1983.

After metamorphosis, growth rates increased in 1980 and 1983 until about 40 mm. At about 40 mm, the growth rates of the two cohorts diverged, and the mean back-calculated growth rate of the 1983 cohort was well below the estimated 95% confidence interval of the 1980 cohort. Growth rates declined steadily in 1983 at sizes larger than 40 mm, while growth rates of about 0.4 mm/d were sustained in 1980 until almost 60 mm. After 60 mm, growth declined at about the same rate as the decline in the 1983

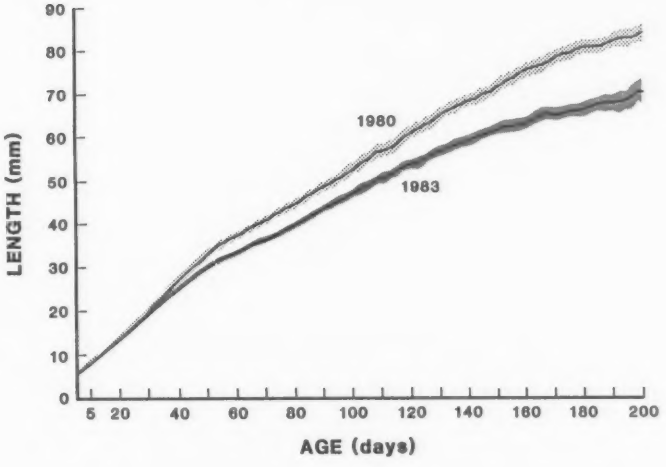

FIGURE 3.—Length versus age of northern anchovy larvae and juveniles of the March 1980 and 1983 cohorts back calculated from daily increments in otoliths.

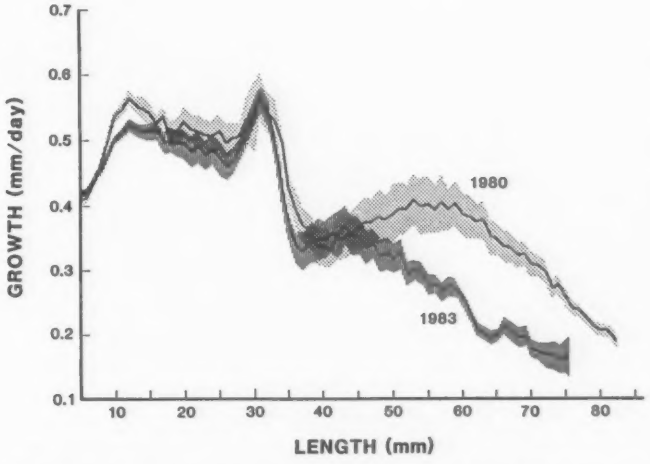

FIGURE 4.—Age-specific growth rates back calculated from daily increment widths of northern anchovy spawned in March 1980 and March 1983. Growth rate of length in mm per day. Shaded areas are 95% confidence intervals.

cohort. Growth within cohorts varied most between 40 and 60 mm.

In 1980 and 1983, northern anchovy growth in weight increased rapidly at small sizes (Fig. 5). Back-calculated growth rates for 1983 reached a local maximum of 6.5 mg/d at about 40 mm and then declined before slowly increasing to 7.5 mg/d at 79 mm. Back-calculated growth rates for 1980 showed a steady increase to about 11.5 mg/d at about 65 mm, which was maintained until about 75 mm, after which growth declined. The growth of northern anchovies hatched in March 1983 peaked at an earlier time (about June) in 1983 and at a smaller size (40 mm), whereas the growth of anchovies hatched in March 1980 peaked near the end of July 1980 and at a larger size at (about 65 mm).

geographic shifts in the population or to changes in spawning date and sampling time in 1984.

When size is adjusted for age and date of spawning, growth of juvenile northern anchovy was reduced in fish hatched in February through April of 1984 compared with fish hatched in the same months in 1980–82 (Fig. 1). This result is consistent with the results from studies of other fish populations on the west coast during El Niño. Growth rates and condition factors were also reduced in the Pacific herring, *Clupea harengus pallasi* (Spratt 1987), the blue rockfish, *Sebastes mystinus* (Van Traskie[2]), and in chinook, *Onchorhynchus tshawytscha*, and coho, *Onchorhynchus kisutch*, salmon (Pearcy and Schoener 1987) during El Niño.

Although the 1982–83 El Nino was fully devel-

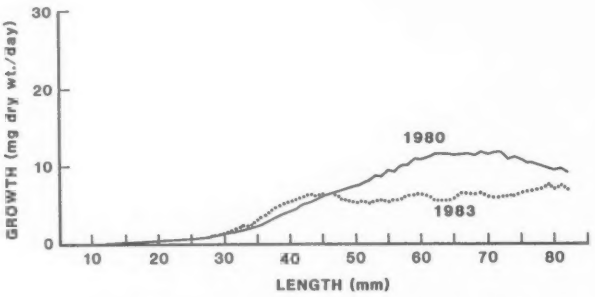

FIGURE 5.—Mean back-calculated growth rates of northern anchovy spawned in March 1980 and March 1983. Growth rate of mass in mg dry weight per day.

DISCUSSION

Growth rates of late larval northern anchovy did not vary in two otherwise extreme years, 1980 and 1983. Methot (1981) found little variance in early larval growth in the sea. Smith (1985) postulated that major changes in recruitment would result from changes in growth rates in the late larval period (10–35 mm) from 0.227 to 0.559 mm/d, a difference of 0.3 mm/d. In this study, however, growth rates of the late larval stage varied by <0.05 mm/d between 1980 and 1983.

Northern anchovy juveniles grew less during 1983 and 1984, compared with the previous three years. Fiedler et al. (1986) also reported reduced growth of anchovy in 1983, but the mean size of 1 yr old fish indicated a dramatic recovery in 1984. This apparent recovery may be in part due to oped by October 1982 along the coast of Peru, full development of large scale warming off the North American coast did not occur until January 1983 (Lynn 1983). Positive temperature anomalies (>1°C) were evident both at the surface and at depth throughout the California Current (McGowan 1985; Norton et al. 1985). Negative salinity anomalies associated with subsurface temperature anomalies indicated intrusion of low salinity water from the south and west into the Southern California Bight (Simpson 1983).

These temperature anomalies represent a large change in the heat content of the ocean but are small relative to the thermal range of northern anchovy. Thus the small size of juvenile

[2]Van Traskie, D. 1985. Growth of blue rockfish (*Sebastes mystinus*) during El Niño. (Abstr.) Calif. Coop. Fish. Invest. Conf., Idyllwild, CA, Oct. 22–25, 1985.

anchovies during 1983 may be a direct result of reduced food availability at the same time that the rapidly growing juveniles experienced higher metabolic rates due to the elevated environmental temperatures. Zooplankton volumes on CalCOFI line 90 (line 90 intersects the coast at lat 33°29.9′N, long. 117°44.4′W and proceeds seaward on a bearing 240° clockwise from North) were lower than the 95% confidence limit of the 30 year CalCOFI time series (McGowan 1985).

Growth rates were not, however, depressed over the entire early life history. The growth rates of larval stages (5–35 mm) were not significantly different between the two years 1982–83 (Figs. 3, 4). Growth rates in 1983 were reduced in the early juvenile stage, and in particular after 40 mm, compared with growth rates in 1980.

Thus food was not growth limiting until the fish reached a certain size. As fish larvae grow, the ration necessary to sustain growth increases. Since the density of food particles decreases with size (Sheldon and Parsons 1967; Sheldon et al. 1972), at some stage food must become growth limiting. Based on this analysis, food-limited growth is unlikely in anchovies <40 mm during conditions that existed in the Southern California Bight in 1983, and unlikely in anchovies <65 mm during "normal" years such as 1980.

The similarity of back-calculated larval growth rates between years may be a result of the interaction of growth and mortality. A wide range of growth rates are possible at this stage (Hunter 1980), but variable growth rates are not observed in the field. Mortality of slow-growing individuals may reduce the range of growth rates in survivors to metamorphosis.

While the 1957–58 El Niño had a dramatic effect on northern anchovy recruitment in 1958, the numbers of fish in the 1983 and 1984 year classes were not appreciably lower than the previous years (Methot 1988). Thus, although the juvenile period was prolonged in 1983, recruitment was not affected. The major effect of El Niño on the anchovy population was to reduce the size of recruits as well as perhaps the size of adults and the reproductive potential of the 1983 and 1984 cohorts.

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Genetic and Morphometric Variation in the Pacific Sardine, *Sardinops sagax caerulea:* Comparisons and Contrasts with Historical Data and with Variability in the Northern Anchovy, *Engraulis mordax*

Dennis Hedgecock, Elmarie S. Hutchinson, Gang Li,
Frederic L. Sly, and Keith Nelson

ABSTRACT: Pacific sardines from five widely separated localities are found to have little genetic variation both within and between populations. Of the 32 allozyme-coding loci examined from a total of 149 fish, the proportions that are polymorphic within a population (P) range from 7% to 27% with a mean of 12%. Average proportions of heterozygous individuals per locus (H_e) range from 0.5% to 1.6% with a mean of 1.0% over the five populations. Pacific sardine populations are virtually genetically identical at the presumptive gene loci examined. For each locus that is polymorphic in more than one population, the same rare variant allele is shared at about the same frequency, suggesting strongly that there has been gene flow throughout the present range of the species. These results contrast with substantial genetic variation detected within and between northern anchovy populations from the California central stock (average P = 40%, average H_e = 7.5%) and with the significantly higher levels of genetic variation reported for other marine clupeoids. Despite a low level of genetic variation, the Pacific sardine shows a north-south cline in size-at-age that is as steep and as large as that seen in historical, precollapse populations. In the past, such differences were interpreted as evidence of genetically distinct subpopulations. Our results imply that rapid differentiation of growth rate among geographic populations, probably together with differentiation of correlated life history traits, is largely environmentally, and not genetically, determined. It appears that biological data from historical populations can safely be used for area-specific fisheries models of the recovering sardine stocks in California.

A variety of studies have suggested that, prior to its collapse in abundance, the Pacific sardine, *Sardinops sagax caerulea*, comprised two or more distinct subpopulations (morphometry and meristics: Hubbs 1925; Clark 1936, 1947; McHugh 1950; growth: Phillips 1948; Felin 1954; Clark and Marr 1955; Radovich 1962, 1982; movements of tagged fish: Clark and Janssen 1945; Clark and Marr 1955; spatiotemporal distribution of spawning: Ahlstrom 1954, 1959; erythrocyte antigens: Sprague and Vrooman 1962; Vrooman 1964; reviews by Marr 1957; Radovich 1982). Population structure likely played a role in the collapse of the fishery, perhaps directly, by virtue of differences among subpopulations in life history and resilience to fishing pressure (Wisner 1961; Murphy 1966; Radovich 1982) and more certainly, indirectly, by contributing to overestimations of stock size in the waning years of the fishery (MacCall 1979). With the return of substantial numbers of Pacific sardines to the California Current in recent years and the lifting of the fishing moratorium (Wolf et al. 1987) has come interest in management questions such as *which* sardine has recovered and what life history characteristics and yields can be expected (MacCall 1986).

We have made studies of protein and morphological variation in the Pacific sardine to shed light on such questions. Electrophoretic separation of proteins followed by chemical staining to reveal the locations of proteins or specific enzymes allows inferences to be made concerning variation in the genes encoding these proteins. This in turn provides a description, useful for management, of the genetic structures of exploited fish populations (see Ryman and Utter 1987). Several clupeoids, including the northern anchovy, *Engraulis mordax*, which co-occurs with the Pacific sardine in the California Current, have been shown to harbor considerable stores of electrophoretically detectable genetic variability (Hedgecock and Li 1983; Table 8). In this paper, we compare protein and allozyme variation in samples of Pacific sardines collected

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from five widely separated localities with that detected by us in nine trawl samples of northern anchovy taken from the central stock (sensu Vrooman et al. 1981).

MATERIALS AND METHODS

Sardinops sagax

Collections

Samples were collected from Guaymas, Sonora, Mexico (February 1985; Fig. 1, GUAYM; N = 48), Magdalena Bay, Baja California Sur, Mexico (May 1984; MAGDA; N = 37), the Southern California Bight (February–April 1986; Huntington Beach, CA, N = 8; San Pedro, CA, N = 28; pooled into one sample, SOCAL), Monterey Bay, CA (November 1984; MONTE; N = 29) and Tomales Bay, CA (December 1984; TOMAL; N = 5). Whole fish were frozen after collection and transported to the Bodega Marine Laboratory where they were kept at −70°C until thawed for morphometric measurements and dissection of tissue samples for electrophoresis.

Morphological Characters

Measurements of the following 12 morphometric traits were made on partially thawed specimens using either vernier caliper or mounted millimeter rule: a series of lengths measured from the snout to the 1) end of the hypural bones (standard length), 2) anterior margin of the orbit, 3) posterior edge of the maxillary, 4) posterior border of the supraoccipital, 5) posterior edge of the operculum, 6) dorsal-fin origin, and 7) vent, followed by measurements of 8) interorbital width, 9) maximum head width, 10) minimum body depth, 11)

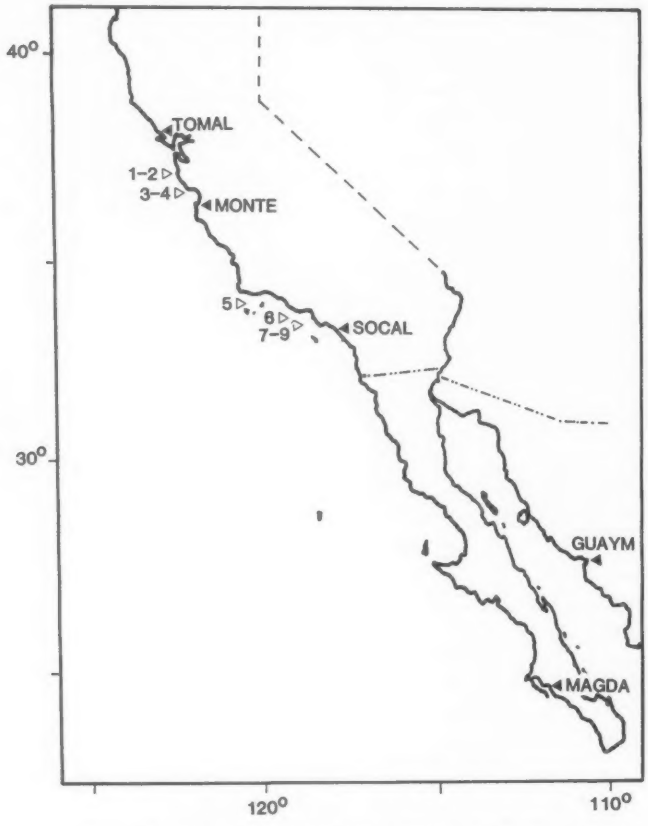

FIGURE 1.—Map showing locations of collections for Pacific sardine (solid arrowheads) and northern anchovy (open arrowheads).

anal-fin-base length, and 12) caudal-peduncle depth.

Tissue Samples

After morphological measurements were made, eye, heart, liver, and skeletal (epaxial) muscle tissues were dissected from each specimen for electrophoretic analyses. Tissue samples were kept in plastic well-trays on ice during dissection, then covered and stored frozen at −70°C for a period of several days prior to electrophoresis. The day before electrophoresis, tissue samples were thawed, equal volumes of 0.5 M Tris-HCl, pH 7.1 buffer were added to the samples, and the tissues were homogenized on ice, by hand, with a ground-glass pestle. Homogenized samples were then returned to the −70°C freezer overnight. On the day of electrophoresis, samples were allowed to thaw slowly on ice.

Otoliths

Sagittal otoliths were removed from specimens and cleared overnight in a 2% KOH solution. They were then rinsed in deionized water for one or more days, air dried, placed by pairs in gelatin capsules with the specimen number, and stored in envelopes labeled by population. Specimen identification for the Magdalena Bay sample was lost.

The age of each specimen was determined by counting otolith annuli following the methods of Collins and Spratt (1969). Each pair of otoliths was placed for examination under water in a separate well (1 cm in diameter and painted black) drilled into a strip of plexiglass. All annuli were counted under a binocular dissection microscope with incident illumination by one of us (F. L. Sly). His recounts agreed with his initial counts (98% consistency); in a comparison test, 80% of his counts were in agreement with those of California State Department of Fish and Game otolith readers.

Electrophoretic Protocol, Genetic Interpretation, and Allozyme Nomenclature

Methods for horizontal starch-gel electrophoresis, protein assays, and genetic interpretation of zymograms were substantially the same as those described previously (Ayala et al. 1973; Tracey et al. 1975; Utter et al. 1987). The protocol used to separate and resolve 20 enzymes or proteins inferred to be encoded by a total of 32 genes is summarized in Table 1. Nomenclatures for proteins, for genes inferred to encode these proteins, and for alleles at these genes are detailed by Utter et al. (1987). Proteins are referred to by the capitalized abbreviations given in Table 1 and the corresponding genes by these same abbreviations italicized in upper and lower case. Numerical suffixes distinguish among isozymes or multiple proteins in order of increasing anodal migration. Alleles are symbolized by italicized numerals obtained by adding or subtracting the number of millimeters separating variants from the most common electromorphs observed for each protein. Alleles encoding common electromorphs are arbitrarily designated *100*. Specimens from several populations were included in every electrophoretic run so that repeated comparisons of relative mobilities of their allozymes were made.

Allozyme Data Analysis

Maximum-likelihood estimates of allelic frequencies and observed proportions of heterozygous genotypes at each locus scored in at least two population samples were computed from numbers of individuals in allelic or genotypic categories and the total numbers of genomes ($2N$) or individuals (N) sampled, respectively. Observed and expected proportions of heterozygous genotypes at each locus were averaged over loci to obtain means (Nei's [1978] unbiased estimates of H_o and H_e, respectively). The proportion of genes for which any electrophoretic variation was detected in a population sample was defined as P; for the population sample sizes used, this criterion of polymorphism is close to the frequently used definition that the most common allele cannot exceed a frequency of 0.99 for a polymorphic locus. Averaging of P and H over population samples was done using angular transformation of these proportional values followed by back-transformation of means and confidence limits. Owing to the nature of the results, no further genetic statistics were calculated.

Morphometric Data Analysis

The BMDP multivariate statistical software package (Dixon 1981) was used to perform discriminant function (P7M) and principal component (P4M) analyses on log-transformed morphometric data. Standard settings were used in the discriminant analysis for tolerance (0.01), F-to-

TABLE 1.—Starch-gel electrophoretic protocols used to reveal allozyme variation.

			Pacific sardine			Northern anchovy		
	Enzyme or protein	E.C. no.	Tissue	Buffer[1]	No. loci	Tissue	Buffer[1]	No. loci
AAT	aspartate aminotransferase	2.6.1.1	—	—	—	E	A	1
ADA	adenosine deaminase	3.5.4.4	L	A	1	L	A	1
ADH	alcohol dehydrogenase	1.1.1.1	E	B	1	—	—	—
ADK	adenylate kinase	2.7.4.3	M	D	2	M	D	1
ALDO	aldolase	4.1.2.13	—	—	—	M	B	1
CK	creatine kinase	2.7.3.2	M	D	1	M	D	1
EST	esterase[2]	3.1.1.–	L	A,B	1	L	A	2
FBP	fructose biphosphatase	3.1.3.11	L	B	1	—	—	—
FUM	fumarate hydratase	4.2.1.2	M	C,D	1	M	D	1
GAPDH	glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	M	C	2	M+E	C	2
GL	dipeptidase[3]	3.4.13.11	E	B	1	—	—	—
GPDH	glycerol-3-phosphate dehydrogenase	1.1.1.8	M	D	1	M	D	1
GPI	glucose-6-phosphate isomerase	5.3.1.9	L,M	D,B	1	L	B	1
HBDH	3-hydroxybutyrate dehydrogenase	1.1.1.30	E+L	B	2	E+L	B	2
HK	hexokinase	2.7.1.1	—	—	—	M	B	1
IDH	isocitrate dehydrogenase	1.1.1.42	H+L	D	2	H	D	1
LAP	leucine aminopeptidase	3.4.11.1	—	—	—	L	A	1
LDH	lactate dehydrogenase	1.1.1.27	L+M	B	2	L+M	B	2
LGG	tripeptidase[4]	3.4.13.4	E	B	1	E,L	B	1
LT	dipeptidase[5]	3.4.13.11	E	B	1	E+L	B	2
MDH	malate dehydrogenase	1.1.1.37	H	D	2	H	D	2
ME	NADP-dependent malate dehydrogenase[6]	1.1.1.40	M	B	1	—	—	—
6PGDH	6-phosphogluconate dehydrogenase	1.1.1.44	E,M	C	1	E,M	C	1
PGM	phosphoglucomutase	2.7.5.1	M	A	1	M	A	1
PNP	purine nucleoside phosphorylase	2.4.2.1	—	—	—	L	E	1
PP	dipeptidase[7]	3.4.13.9	L	B	1	—	—	—
PROT	general proteins[8]	general	E+M	A	4	E+M	A	9
SOD	superoxide dismutase[9]	1.15.1.1	L	B	1	L	B	1
TPI	triosephosphate isomerase	5.3.1.1	—	—	—	M	D	1
XDH	xanthine dehydrogenase	1.1.1.204	—	—	—	L	B	1
	Totals[10]		20 proteins,		32 loci	24 proteins,		39 loci

[1]Buffers A, B, C, and D as described by Tracey et al. (1975); buffer E is the lithium borate discontinuous buffer system 2 of Selander et al. (1971).
[2]α-naphthyl butyrate and β-naphthyl acetate as substrates.
[3]L-glycyl-leucine as substrate.
[4]L-leucyl-glycyl-glycine as substrate.
[5]A 1:1 mixture of L-leucyl-valine and L-leucyl-tyrosine as substrates.
[6]Known as malic enzyme.
[7]L-phenylalanyl-proline as substrate.
[8]Stained with Coomassie blue.
[9]Usually scored on gels stained for HBDH.
[10]Di- and tripeptidases counted as one enzyme in totals.

enter (4.000), F-to-remove (3.996), and prior probabilities (equal).

Engraulis Mordax

Collections

Samples of 48 anchovies were obtained from each of nine midwater trawl stations (Fig. 1) occupied between the nights of 24 January and 1 February 1982, by CalCOFI cruise 8202 aboard the RV *David Starr Jordan* of NOAA Southwest Fisheries Center, La Jolla. CalCOFI grid coordinates (CalCOFI Atlas No. 1, 1963) for these collections and place names assigned to them for convenience were as follows: 1) Half Moon Bay, 63.3:51.0; 2) Half Moon Bay, 63.3:52.0; 3) Santa Cruz, 66.7:49.0; 4) Santa Cruz, 66.7:50.0; 5) Santa Barbara, 81.3:42.4; 6) Point Dume, 85.0:44.0; 7) Santa Monica Bay, 85.8:34.0; 8) Santa Monica Bay, 85.8:36.0; 9) Santa Monica Bay, 85.8:41.0. Whole fish were frozen individually aboard ship at −70°C and then packaged in plastic bags labeled by locality. Frozen packages were shipped by air to the Bodega Marine

Laboratory where they were kept in a −70°C freezer until dissection.

Data Taken on Specimens

Eye, heart, liver, and skeletal muscle tissue samples were taken from each of the 432 northern anchovy used for this study. For all specimens but those from population sample 8, standard length and sex were recorded and otoliths were taken. Annuli were counted by one of us (F. L. Sly) in a manner similar to that described for the sardine, following the methods of Collins and Spratt (1969).

The electrophoretic protocol used to separate 24 proteins encoded by 39 scorable genes is given in Table 1. These proteins were assayed in tissue samples from an average of nearly 46 specimens (minimum of three) from each of the 9 population samples. Genetic interpretation and allozyme nomenclature were as described above for the sardine analysis with the following additions: 1) Gels for polymorphic enzymes were scored independently by the authors D. Hedgecock and Gang Li, and any discrepancy between the two scores was resolved by reexamination and negotiation; and 2) problems with the resolution of certain allozymes from liver tissue became apparent. A pattern of missing IDH-2, missing EST-5, and blurred LDH-3 and HBDH-2 phenotypes—the last mimicking the 100/105 polymorphism—was subsequently associated with degenerated liver tissues in individual specimens or even entire population samples that were, perhaps, not frozen soon enough after trawling. IDH-2 appeared most sensitive to this and was eliminated from the study, except as an indicator of degenerate liver tissue. To correct for potential bias in *Hbdh-2* data, individual HBDH-2 scores were omitted if (i) any other element of the above composite, degenerate-liver zymogram was observed in that individual *and* (ii) missing elements (i.e., IDH-2 and EST-5) were observed in at least one other specimen from the same population sample (to prevent a missing or failed enzyme assay from causing data rejection). Mean number of individuals assayed for HBDH per population sample was thus reduced to 33 ± 3.

Allozyme Data Analysis

Single-individual genotypes were recoded as paired alphabetical characters and submitted to the BIOSYS-1 program of Swofford and Selander (1981) for calculations of allelic frequencies, average proportions of heterozygous individuals per locus (H_o and H_e as defined above), proportions of polymorphic genes (P, where a locus is considered polymorphic if the frequency of the most common allele does not exceed 0.99), chi-square goodness-of-fit tests to Hardy-Weinberg-Castle (H-W-C) equilibrium genotypic proportions using Levene's (1949) correction for small sample sizes, Wright's (1978) F-statistics, and Nei's (1978) unbiased estimates of average genetic identity (I) and genetic distance (D). Averaging of P and H over population samples was done using angular transformation followed by back-transformation of means and confidence limits. Spearman rank correlations of angular-transformed allelic frequencies with the sines of latitude of collection localities, log-likelihood ratio (G) tests of the independence of allelic frequency and locality, and analyses of allelic frequencies cross-classified by locality, sex, and age (ACCCD; Fienberg 1980) were used to evaluate sources of genetic heterogeneity.

RESULTS

Sardinops sagax caerulea

Genetic Variation

We detected electrophoretic variation in the zymograms of seven proteins, including three di- and tripeptidases, from Pacific sardines, (EST-6, FBP, GPDH, IDH-2, LGG, LT, PP, 6PGDH, SOD; Table 2B). There is, however, remarkably little protein polymorphism and individual heterozygosity at the total 32 loci examined in 149 Pacific sardines (Table 2A). The proportion of polymorphic genes ranges from 7.4% in each of the samples from Tomales and Magdalena Bays to 26.9% in the Guaymas sample, with an average of 12.3% (95% C.L.: 6.4–19.6%). Average heterozygosities range from 0.5% in the Magdalena Bay sample to 1.7% in the Guaymas sample, with a mean over all population samples of 1.0% (95% C.L.: 0.6–1.5%). Estimates of genetic variation are probably best for the Guaymas sample, for two reasons: 1) There were generally larger numbers of individuals sampled per gene, which accounts for the finding of rare heterozygotes at *Idh-2*, *Lgg*, and *Pp*, loci that were not well sampled elsewhere. 2) We sampled two moderately polymorphic loci, *Est-6* and *Fbp*, that were not scored in any other large population sample. There are no significant differences between

TABLE 2.—Allozyme variation in five population samples of Pacific sardine.

	Tomales Bay	Monterey Bay	S. Calif. Bight	Magdalena Bay	Guaymas
A. Summary statistics					
No. of fish (N)	5	29	30	37	48
No. of loci	27	27	23	27	26
P (as percent)	7.4	14.8	8.7	7.4	26.9
H_o (as percent)	1.5	1.0	0.6	0.5	1.7
H_e (as percent)	1.5	1.0	0.6	0.5	1.6

B. Polymorphic enzymes[1]

	Variants	No. of heterozygotes in samples of size (N)				
EST-6	(103)	0 (5)	—	—	—	3 (48)
FBP	(102)	1 (5)	—	—	—	7 (47)
GPDH	(102)	0 (2)	1 (29)	0 (30)	0 (34)	0 (12)
IDH-2	(93)	0 (5)	0 (22)	1 (29)	0 (23)	1 (48)
LGG	(96)	0 (5)	—	0 (30)	0 (7)	1 (48)
LT	(97)	0 (5)	—	0 (30)	0 (7)	1 (48)
PP	(103)	0 (5)	3 (28)	0 (30)	1 (37)	4 (48)
6PGDH	(103+98)	1 (5)	3 (29)	3 (30)	4 (37)	3+1 (48)
SOD	(93)	0 (5)	1 (29)	0 (30)	0 (37)	0 (48)

[1]Zymogram banding patterns of presumptive heterozygotes at the loci inferred to encode these proteins conform to those expected on the basis of known subunit structures: tetrameric structure for FBP; dimeric structure for GPDH, IDH, LGG, 6PGDH, and SOD; monomeric structure for EST-6, LT and PP (Darnall and Klotz 1975; Harris and Hopkinson 1976; Ruth and Wold 1976; Koehn and Eanes 1978; Utter et al. 1987).

observed and expected average heterozygosities in any of the population samples. For no individual locus is it possible to test H-W-C expected genotypic proportions in a population sample, owing to the low frequencies of variant alleles and the relatively small sample sizes.

In addition to the low genetic variation within each of the samples of Pacific sardines, there is almost no variation among populations in the frequencies of allozymes (Table 2B). Except for 6PGDH, for which a third allozyme was inferred from observation of a single 98/103 heterozygous phenotype in the Guaymas sample, all polymorphic allozymes are represented by just two alleles. For each locus that is polymorphic in more than one population, the same rare variant allele is shared at about the same frequency (Table 2B). Thus, the five, widely separated populations of Pacific sardine sampled in our study are virtually genetically identical at the 32 loci examined.

Ageing from Otolith Annuli

Under the assumption that an annulus represents a yearly growth ring and that fish with one ring are one year old, three age classes, 1's, 2's, and 3's, predominate in all five population samples. There are no statistically significant differences in distribution of ages among the four larger samples $\chi^2_{9df} = 10.7083$, $0.1 < P < 0.5$; data in Table 3). Nor is there a difference between the small Tomales Bay sample and the others (Fisher's exact test on Tomales Bay data versus all other data combined, $P > 0.90$).

TABLE 3.—Distributions of ages in five population samples of Pacific sardine.

Age	Tomales Bay	Monterey Bay	S. Calif. Bight	Magdalena Bay	Guaymas
1	0	9	10	19	21
2	4	14	14	13	22
3	1	3	5	1	3
4	0	0	1	0	0
Sample size:	5	26	30	33	46
Mean:	2.2	1.8	1.8	1.5	1.6

Morphological Variation

In contrast to the similarity of age class compositions among population samples, size distributions among sites are grossly different, with sardines from California being much larger than those from Mexico (Fig. 2). Stepwise discriminant function analysis (DFA) of the 12 log-transformed morphometric variates reveals, after 10 steps, significant differences among the five population samples (approximate F = 22.085 with 32, 499 df, $P << 0.001$). However, discrimination is based primarily on log of standard length which enters the discriminant function first with F = 243.49 ($P << 0.001$; 4, 142 df). A principal component analysis (PCA) of those traits contributing to between-group variance in the DFA produces a single factor, heavily and positively loaded by all traits and accounting for 97% of the variance in data space (minimum factor eigenvalue set to 1.0); such a factor is generally interpreted to represent variance in size (Humphries et al. 1981). The evident geographic cline in size apparently reflects a cline in growth rate; at the extremes, fish of the same age from central California and from the Gulf of California can differ in standard length by nearly 100 mm (see Figure 2).

Two further analyses do indicate minor but significant morphological variation attributable to shape differences among sardines from different geographic areas. First, two factors extracted in a PCA of log-transformed variates standardized by subtraction of the log of standard length show complementary patterns of factor loadings suggestive of different allometries of head size relative to body size among populations (Fig. 3A). The separation of populations along the factor 1 axis (Fig. 3B) is *inversely* related to standard length; i.e, larger California fish are on the left of smaller Mexican fish, owing to the negative allometry of head dimensions relative to standard length. This result is consistent with observations on postlarval Pacific sardines (McHugh 1950) as well as with a general geographical pattern in fish morphology (Jensen 1944; Martin 1949).

Second, comparisons of pairs of population samples for which there is considerable overlap in the sizes of specimens (Southern California

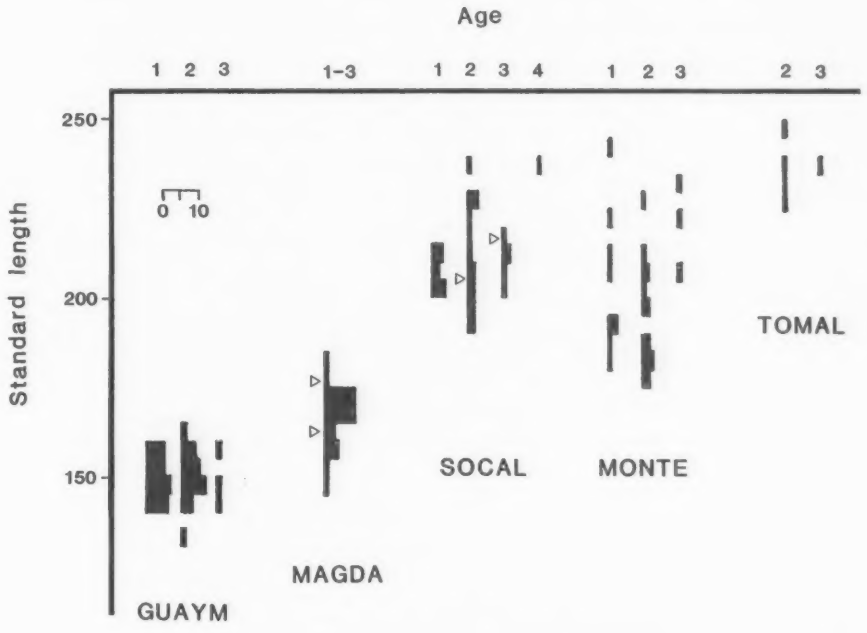

FIGURE 2.—Histograms of standard lengths for various ages of Pacific sardines in five population samples. Open arrowheads along the baselines of the Magdalena Bay and Southern California Bight population samples indicate the mean sizes of two- and three-year-old fish in the 1961–62 sardine catches of Baja California and California, respectively (from Vrooman 1964).

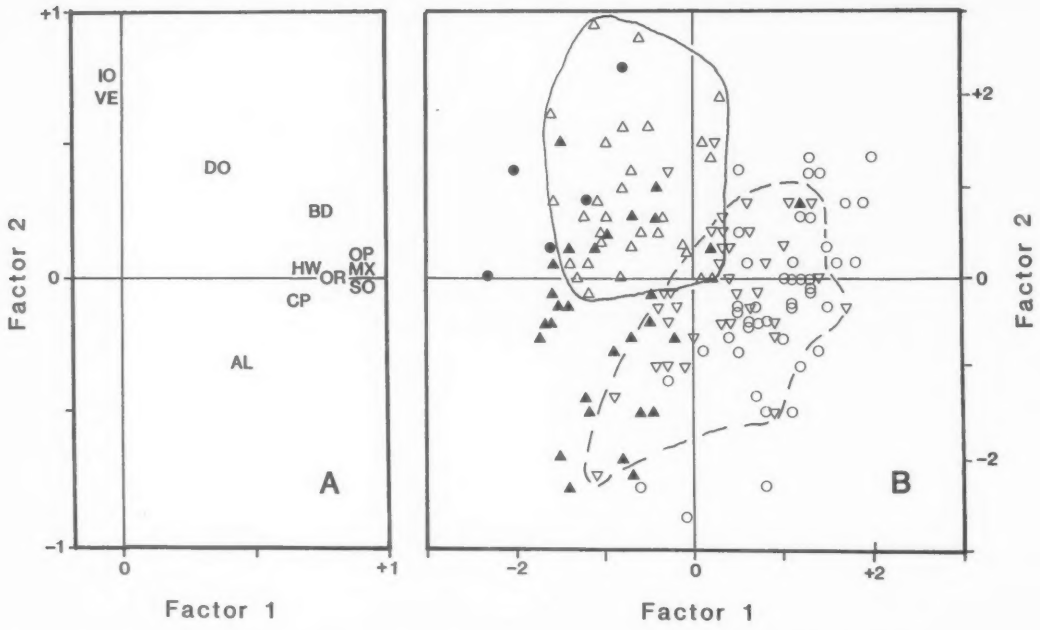

FIGURE 3.—(A) Loadings on the first two factors from a principal components analysis of size-standardized morphometric traits measured on 147 Pacific sardines; I0 = interorbital width, VE = snout to vent length, DO = snout to dorsal-fin origin, AL = anal-fin base length, CP = caudal-peduncle depth, HW = maximum head width, BD = minimum body depth, OR = snout to orbit length, OP = snout to operculum length, MX = snout to maxillary length, SO = snout to supraoccipital length. (B) Scores for individual sardines on these first two factors. Open triangles, solid line: SOCAL; open inverted triangles, dashed line: MAGDA. Other populations are solid circles, TOMAL; solid triangles, MONTE; open circles, GUAYM (see Figure 1).

Bight vs. Monterey Bay and Magdalena Bay vs. Guaymas) also show variation in head : body-size allometry. A standard length range of 192–240 mm defines a subset of the Monterey Bay sample comprising 17 individuals whose mean length is identical to that of the 30 southern California specimens. DFA of log-transformed variates takes two steps to produce significant between-group variance (F = 13.344, $P << 0.001$; 2, 44 df) and an average percent correct assignment in a posteriori classifications of 77% (Table 4A). The two characters used in the classification functions are interorbital width and head width (Table 4A). Between subsets of similarly sized fish (145–162 mm) from Guaymas (N = 37) and Magdalena Bay (N = 11), DFA of nine log-transformed variates (three were discarded to keep the number of variates less than N = 11 for Magdalena Bay) produces significant variance in three steps (F = 17.568, $P << 0.001$; 3, 44 df) and 90% correct classification (Table 4B). Maxillary length, interorbital width, and length of anal-fin base contribute to the classification functions for these two Mexican populations (Table 4B).

Engraulis mordax

Genetic Variation Within Populations

Electrophoretic variation was detected in all northern anchovy proteins examined except ALDO and CK. From this variation in protein phenotypes, we infer that our samples of northern anchovy populations contain substantial levels of individual genetic variation (Table 5). Over the 39 loci examined, the average number of alleles per locus per population is 1.61 ± 0.02, ranging from 1.49 ± 0.13 in the inshore Half Moon Bay sample to 1.72 ± 0.16 in the offshore Santa Cruz sample. Proportions of polymorphic loci per population range from 33.3% in the inshore Half Moon Bay sample to 46.2% in the middle station of the Santa Monica Bay transect; mean P over the nine samples is 39.8% (95% C.L.: 37.2–42.5%). Average expected hetero-

TABLE 4.—Classification functions and a posteriori (jackknifed) classifications from discriminant function analyses of similarly sized Pacific sardines from (A) California and (B) Mexican population samples.

A. California's classification functions:

Variate	Monterey	S. Calif. Bight
log interorbital	−668.284	−597.504
log head width	2437.560	2357.524
constant	−1311.788	−1274.079

Population sample (192–240 mm)	% correct classification	Cases classified in sample		
		Monterey	S. Calif. Bight	*N*
Monterey Bay	82.4	14	3	17
S. Calif. Bight	73.3	8	22	30

B. Mexico's classification functions:

Variate	Guaymas	Magdalena Bay
log maxillary	3061.400	2871.099
log interorbital	−449.694	−537.635
log anal-fin base	521.755	591.291
constant	−2006.101	−1949.291

Population sample (145–162 mm)	% correct classification	Cases classified in sample		
		Guaymas	Magdalena Bay	*N*
Guaymas	89.2	33	4	37
Magdalena Bay	90.9	1	10	11

zygosities range from 6.9% in the inshore Half Moon Bay and Point Dume samples to 8.0% in the middle Santa Monica Bay sample, with a mean over the nine samples of 7.5% (95% C.L.: 7.1–7.9%). There are no significant differences between observed and expected average heterozygosities in any of the samples.

Sample sizes and levels of polymorphism permit goodness-of-fit tests to H-W-C genotypic proportions in 27 cases, involving five loci—*Fum*, *Hbdh-2*, *Lgg*, *Pgm*, and *Xdh*. Prior to 14 of these tests, rare alleles were pooled and the frequencies of composite genotypic classes recalculated accordingly (Pamilo and Varvio-Aho, 1984). The probability assigned to a significant deviation from the H-W-C (null) hypothesis, $P_{\alpha 0.05}$, was adjusted for multiple testing by dividing $\alpha_{0.05}$ by the number of populations over which a given locus was simultaneously tested (Cooper 1968). None of the 27 tests is significant at the adjusted $\alpha_{0.05}$ level, although chi-square values for *Hbdh-2* in the offshore Santa Cruz sample and for *Lgg* in the Point Dume sample come close.

Deviations from H-W-C equilibrium for *Hbdh-2* and *Lgg* tend towards excess heterozygotes. Wright's (1978) fixation indices (F_{IS}) for *Hbdh-2* in population 4 and for *Lgg* in populations 4, 6, and 8 (four chi-square tests with $P \leq 0.06$) are −0.49, −0.37, −0.36, and −0.19, respectively. Averaged over populations and alleles, F_{IS} for *Hbdh-2* and *Lgg* is −0.13 and −0.175, respectively; the weighted average F_{IS} over all loci is −0.045 (see Table 7). There is, owing to these excesses of heterozygotes within population samples, an overall excess of heterozygotes in the total population sampled (mean F_{IT} over all loci and populations is −0.012), despite divergence among populations (next section), which is expected to reduce heterozygosity (Wahlund 1928).

Genetic Variation Between Populations

Eleven loci were polymorphic enough throughout the nine population samples (Table 6) to permit analyses of geographical heterogeneity in allelic frequencies. Rare alleles were pooled into one class for all but the *Lgg* and *Xdh* loci, for which two rare-allele classes were formed. The resulting two- or three-by-nine matrices were tested for r × c independence by log-likelihood

TABLE 5.—Summary statistics for three measures of genetic diversity in northern anchovy.

Population sample (CalCOFI grid no.)[1]	Mean sample size per locus (SE)	Mean no. alleles per locus (SE)	% loci polymorphic	Mean heterozygosity	
				Observed (SE)	Expected (SE)
1. Half Moon Bay (63.3:51.0)	44.1 (1.4)	1.49 (0.13)	33.3	7.6 (2.6)	6.9 (2.3)
2. Half Moon Bay (63.3:52.0)	45.7 (1.0)	1.59 (0.14)	35.9	7.9 (2.6)	7.3 (2.3)
3. Santa Cruz (66.7:49.0)	45.4 (1.1)	1.51 (0.11)	41.0	7.1 (2.3)	7.6 (2.4)
4. Santa Cruz (66.7:50.0)	46.3 (0.8)	1.72 (0.16)	41.0	8.70 (2.4)	8.0 (2.5)
5. Santa Barbara (81.3:42.4)	45.9 (1.3)	1.64 (0.17)	35.9	7.9 (2.5)	7.3 (2.3)
6. Point Dume (85.0:44.0)	46.6 (1.1)	1.59 (0.14)	41.0	6.9 (2.5)	6.9 (2.3)
7. Santa Monica Bay (85.8:34.0)	46.3 (0.8)	1.64 (0.14)	43.6	8.1 (2.6)	7.8 (2.4)
8. Santa Monica Bay (85.8:36.0)	42.6 (1.7)	1.67 (0.13)	46.2	8.7 (2.5)	8.8 (2.4)
9. Santa Monica Bay (85.8:41.0)	46.8 (0.4)	1.62 (0.14)	41.0	6.9 (2.2)	7.3 (2.3)
Averages: (SE or 95% C.L.)	45.5 (0.5)	1.61 (0.02)	39.8 (37.2-42.5)	7.8 (7.3-8.2)	7.5 (7.1-7.9)

[1]California Cooperative Oceanic Fisheries Investigations (1963).

TABLE 6.—Frequencies of allozymes for 11 polymorphic enzymes[1] in northern anchovy samples.

Locus (*N*) Alleles	Population samples								
	1	2	3	4	5	6	7	8	9
Est-5									
(*N*)	44	48	37	47	44	48	41	22	40
98	0.011	0.0	0.0	0.011	0.011	0.01	0.061	0.0	0.013
100	0.966	0.948	0.973	0.957	0.955	0.948	0.915	0.909	0.925
101	0.0	0.0	0.0	0.011	0.0	0.021	0.012	0.0	0.025
102	0.023	0.042	0.027	0.021	0.023	0.021	0.012	0.091	0.038
103	0.0	0.01	0.0	0.0	0.011	0.0	0.0	0.0	0.0
Fum									
(N)	48	48	48	48	48	48	48	47	48
96	0.021	0.0	0.01	0.01	0.0	0.0	0.01	0.0	0.0
100	0.5	0.615	0.479	0.573	0.458	0.51	0.573	0.585	0.49
104	0.479	0.385	0.51	0.417	0.542	0.49	0.417	0.415	0.51
Gpi									
(*N*)	48	48	48	48	48	48	48	47	48
90n	0.0	0.0	0.0	0.0	0.0	0.01	0.01	0.0	0.0
96	0.0	0.0	0.0	0.01	0.021	0.01	0.01	0.0	0.01
100	0.979	0.969	0.958	0.958	0.958	0.969	0.958	0.798	0.927
103	0.021	0.021	0.042	0.01	0.01	0.01	0.0	0.202	0.042
105	0.0	0.01	0.0	0.021	0.01	0.0	0.021	0.0	0.021

TABLE 6.—*Continued.*

Locus (*N*) Alleles	Population samples								
	1	2	3	4	5	6	7	8	9
Hbdh-1									
(*N*)	48	48	48	48	48	48	48	48	48
90	0.0	0.01	0.0	0.0	0.0	0.0	0.0	0.0	0.0
92	0.01	0.0	0.0	0.0	0.01	0.0	0.0	0.0	0.0
96	0.042	0.0	0.0	0.021	0.042	0.042	0.0	0.0	0.02
98	0.01	0.031	0.021	0.021	0.01	0.0	0.031	0.021	0.0
100	0.938	0.948	0.979	0.958	0.927	0.958	0.969	0.979	0.979
103	0.0	0.01	0.0	0.0	0.01	0.0	0.0	0.0	0.0
Hbdh-2									
(*N*)	28	29	32	32	41	48	31	17	40
100	0.821	0.741	0.547	0.516	0.732	0.927	0.597	0.765	0.837
105	0.179	0.259	0.453	0.484	0.268	0.073	0.403	0.235	0.162
Ldh-1									
(*N*)	48	48	48	48	48	48	48	48	48
96	0.115	0.208	0.188	0.125	0.198	0.198	0.125	0.146	0.135
100	0.885	0.792	0.813	0.875	0.802	0.802	0.875	0.854	0.865
Lt-1									
(*N*)	48	48	48	48	48	48	48	48	48
96	0.0	0.021	0.0	0.021	0.01	0.0	0.0	0.021	0.01
100	0.948	0.958	0.948	0.938	0.948	0.99	0.969	0.885	0.938
103	0.052	0.021	0.052	0.042	0.042	0.01	0.031	0.094	0.052
Lgg									
(*N*)	48	48	48	48	48	48	48	48	48
97	0.021	0.021	0.083	0.01	0.042	0.021	0.031	0.052	0.0
100	0.646	0.66	0.74	0.604	0.708	0.583	0.563	0.583	0.688
104	0.333	0.319	0.177	0.385	0.25	0.385	0.365	0.365	0.313
107	0.0	0.0	0.0	0.0	0.0	0.01	0.042	0.0	0.0
6Pgdh									
(*N*)	48	48	48	48	48	48	48	48	48
98	0.021	0.01	0.021	0.052	0.0	0.0	0.0	0.01	0.021
100	0.979	0.979	0.969	0.948	0.99	1.0	0.969	0.958	0.979
104	0.0	0.01	0.01	0.0	0.01	0.0	0.031	0.031	0.0
Pgm									
(*N*)	48	48	48	47	48	48	48	48	48
96	0.0	0.01	0.0	0.01	0.0	0.01	0.0	0.0	0.0
98	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01	0.0
100	0.708	0.677	0.74	0.667	0.771	0.76	0.813	0.833	0.844
103	0.292	0.313	0.26	0.323	0.229	0.229	0.188	0.156	0.156
Xdh									
(*N*)	48	48	48	48	48	48	48	39	48
98	0.177	0.125	0.031	0.167	0.156	0.281	0.135	0.0	0.365
100	0.792	0.844	0.854	0.823	0.823	0.719	0.792	0.744	0.604
102	0.031	0.031	0.115	0.01	0.021	0.0	0.073	0.256	0.031

[1]Zymogram banding patterns of presumptive heterozygotes conform to those expected on the basis of known subunit structures: tetrameric structure for FUM and LDH-1; dimeric structure for GPI, HBDH-1, HBDH-2, LGG, and 6PGDH; monomeric structure for EST-5, LT-1 and PGM; XDH not separated well enough to confirm tetrameric structure (see Table 2 for references).

ratios (G, Table 7). For five of the 11 loci, allelic frequencies are significantly nonindependent of locality; significant heterogeneity of allelic frequencies corresponds to F_{ST} values ≥ 0.019. Considering just the 11 polymorphic loci, Nei's (1978) unbiased genetic identity and distance statistics for 36 pairs of population samples average 0.992 ± 0.001 and 0.008 ± 0.001, respectively; over all 39 loci these statistics average 0.998 ± 0.0003 and 0.002 ± 0.0003, respectively.

Further analyses show that some of the heterogeneity in allelic frequencies is geographically patterned, some is associated with genetic differences between the sexes and among age classes, but that most is not associated with any obvious environmental or biological factor. Allelic frequencies at two of the five variable loci, *Pgm* and *Xdh*, are significantly correlated with latitude (Fig. 4). An attempt was made to examine the dependence of gene frequencies on sex and age as well as locality, but analyses of cross-classified data are made difficult by small sample sizes and uneven distributions of sexes and age classes over localities. In tests of three-factor (LOCALITY × SEX × ALLELIC FREQUENCY) log-linear models for *Hbdh-2*, *Lgg*, *Pgm* and *Xdh*, sex was found to be associated with ALLELIC FREQUENCY only for *Hbdh-2*, for which a fully saturated model with all three pairwise interactions among factors appeared to be the best fit. In 15 tests of log-linear models of AGE × SEX × ALLELIC FREQUENCY within individual population samples, only four could *not* be fit by the model of complete factor independence (*Hbdh-2* in population 9, *Lgg* in population 4, *Pgm* in populations 3 and 4). AGE and ALLELIC FREQUENCY were associated only for *Pgm* in the inshore Santa Cruz sample, for which, again, a fully saturated model was the best fit. Interestingly, interactions of AGE and SEX independent of (or only conditionally associated with) ALLELIC FREQUENCY were significant in all four cases; an association of older males with younger females appeared to be responsible for this.

TABLE 7.—F-statistics and log-likelihood ratio (G) tests of allelic frequency x locality independence for polymorphic loci in nine population samples of northern anchovy.

Locus	F_{IS}	F_{IT}	F_{ST}	G	df	Sig.[1]
Est-5	0.083	0.095	0.012	5.53	8	ns
Fum	0.006	0.019	0.013	11.21	8	ns
Gpi	0.069	0.123	0.057	31.14	8	***
Hbdh-1	−0.040	−0.027	0.012	8.05	8	ns
Hbdh-2	−0.130	−0.037	0.082	57.66	8	***
Ldh-A	0.043	0.051	0.008	7.28	8	ns
Lt-1	0.033	0.046	0.013	13.06	8	ns
Lgg	−0.175	−0.153	0.019	37.98	16	**
6Pgdh	−0.036	−0.021	0.015	11.19	8	ns
Pgm	−0.067	−0.047	0.019	16.68	8	*
Xdh	0.006	0.067	0.062	130.15	16	***
Means:	−0.045	−0.012	0.032			

[1]Probability levels for significance of G-tests are * = $0.01 < P < 0.05$; ** = $0.001 < P < 0.01$; *** = $P < 0.001$.

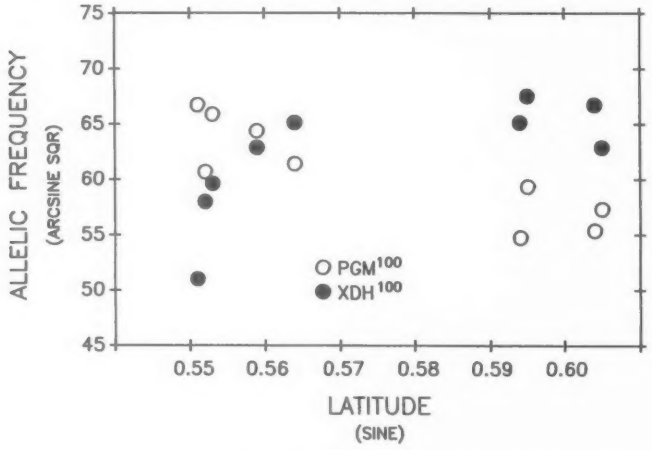

FIGURE 4.—Frequencies of the common alleles for *Pgm* and *Xdh* (arcsine-square-root transformed) plotted against the sine of latitude of collection site. Spearman rank correlation coefficients for the two loci are $r_S = -0.783$, $t = -3.330$ for *Pgm* and $r_S = 0.812$, $t = 3.681$ for *Xdh*.

DISCUSSION

Low Genetic Variation in the Pacific Sardine

Relative to other clupeoids, the Pacific sardine, *Sardinops sagax*, is depauperate in allozyme variation. Direct comparison with the northern anchovy, *Engraulis mordax*, in this study shows that the Pacific sardine has less than 25% of the average heterozygosity of the northern anchovy (Table 2A vs. Table 5). The northern anchovy, not the Pacific sardine, appears to have levels of variation typical of those reported in allozyme studies of clupeoids (Table 8). Average heterozygosity for 15 marine species of the order Clupeiformes is 7.1% (95% C.L.: 6.0–8.2%). The average expected heterozygosity for the Pacific sardine, 1.0%, and even the slightly greater heterozygosity found in the Guaymas population sample, 1.6% fall significantly below the clupeoid distribution ($z = -4.02$, $P < 0.000033$ and $z = -3.39$, $P < 0.0003$, respectively).

There is so little variation within and between Pacific sardine populations that it is not possible to test whether distributions of genotypes conform to the expectations of random mating or whether allelic frequencies are heterogeneous throughout the range of populations sampled. That sardines in widely separated localities have the same rare alleles (Table 2B) suggests strongly, however, that there has been substantial gene flow among contemporary populations (Slatkin 1985).

TABLE 8.—Allozyme variation reported for marine species of the order Clupeiformes.

Species	No. of pops studied	No. of loci studied	Mean no. alleles per locus	Percent loci polymorphic[1]	% mean heterozygosity Obs.	% mean heterozygosity Exp[2]	References[3]
Clupeidae							
Clupeinae							
Opisthonema							
bulleri	2	29	1.4	20.7	5.4	5.5	(1)
medirastre	2	29	1.3	27.6	8.5	7.7	(1)
libertate	5	29	1.6	31.0	6.3	6.7	(1)
Sardinops							
sagax	5	27	1.4	14.5	1.0	1.0	this study
melanosticta	1	22	—	22.7	6.4	—	(2)
Clupea							
harengus	6	40	—	47.5	—	6.5	(3)
harengus	3	25	1.8	38.8	—	7.0	(4)
harengus	14	42	—	21.3	4.8	—	(5)
pallasi	21	40	—	65.0	—	8.3	(6)
pallasi	1	17	—	29.4	5.8	—	(2)
Sprattus							
antipodum	2	13	1.7	50.0	9.6	11.2	(7)
sp.	1	13	1.6	46.2	5.5	5.7	(7)
Dussumieriinae							
Spratelloides							
gracilis	2	16	1.5	24.7	4.0	—	(8)
sp.	2	14	1.5	32.1	4.6	—	(8)
Engraulidae							
Engraulinae							
Engraulis							
japonicus	1	22	—	36.4	6.7	—	(2)
capensis	31	31	—	48.3	—	11.5	(9)
mordax	9	39	1.6	39.8	7.7	7.5	this study
Stolephorus							
heterolobus	3	18	1.7	22.2	10.1	—	(8)
devisi	3	19	1.7	17.1	6.8	—	(8)

[1]Polymorphism defined either as $P_{0.99}$ or inclusive of all observed variation.
[2]H_e are either unbiased estimtes (Nei 1978) or simple averages.
[3](1) Hedgecock et al. 1988; (2) Fujio and Kato 1979; (3) Grant 1984; (4) Andersson et al. 1981; (5) Kornfield et al. 1982; (6) Grant and Utter 1984; (7) Smith and Robertson 1981; (8) Daly and Richardson 1980; (9) Grant 1985a.

By contrast, the substantial allozyme polymorphism in the northern anchovy allows tests of both random mating and spatial homogeneity of allelic frequencies. Chi-square goodness-of-fit tests detect no significant departures from the genotypic proportions expected under random mating, although substantial excesses of heterozygotes are found at the *Hbdh-2* and *Lgg* loci. While liver-tissue degradation may have contributed to this result for *Hbdh-2* (see Materials and Methods), this explanation cannot hold for *Lgg*, which was scored reliably from both liver and eye zymograms. Differences in allelic frequencies either among age classes or between sexes can produce excess heterozygosity, and significant interaction of sex and allelic frequency is detected by fitting of log-linear models to *Hbdh-2* data. For *Lgg*, on the other hand, sex and allelic frequency are independent given locality. It must be remembered that the chi-square test of Hardy-Weinberg-Castle equilibrium has little power to detect failure of its basic assumptions, notably no selection at the locus and an infinite, unsubdivided population (Wallace 1958; Lewontin and Cockerham 1959).

The northern anchovy, again in contrast to the Pacific sardine, appears to have a complex population structure as evidenced by significant heterogeneity of allelic frequencies at 5 of 11 polymorphic loci (Table 7), correlations of some alleles with latitude (Fig. 4), and dependence of some allelic frequencies on sex and age. This heterogeneity is unexpected. All samples were collected within the area occupied by the central stock, which has been considered a single, randomly mating population, primarily on the basis of transferrin-allele frequencies and meristic data (Vrooman et al. 1981; see MacCall et al. 1983). Differences among populations within this area have nevertheless been described for growth and age composition (Parrish et al. 1985), size-adjusted otolith weight (Spratt 1972), size at age (Collins 1969; Mais 1974; Mallicoate and Parrish 1981), seasonality of spawning (Mais 1974; Parrish[1]), and migration patterns (Haugen et al. 1969; Mais 1974), together with between-year variation in many of these life history traits. Similar genetic heterogeneity of anchovy stocks has been described for *Engraulis encrasicholis* (Altukhov et al. 1969a, b; Dobrovolov 1978), although homogeneity of allelic frequencies was reported by Grant (1985b) for *E. capensis*.

For loci polymorphic over the nine population samples, Wright's (1978) measure of average genetic variance among populations, F_{ST}, and Nei's (1978) average genetic distance D—two measures that are maximized by allele replacement among populations—are both relatively small: 0.032 and 0.008, respectively. Significant heterogeneity of allelic frequencies without substantial allele replacement may reflect population subdivision and differentiation resulting from ecological, rather than historical processes. We will explore the causes of this paradoxical genetic heterogeneity in subsequent reports drawing on much larger sets of allozyme, sex, age, and morphological data for northern anchovy collected between 1982 and 1985.

Why does the Pacific sardine have low genetic variation? One possibility is that this species originally had levels of variation typical of clupeoids, but that much of this was lost in the collapse of the California sardine fishery in the 1950's and early 1960's. That this fishery collapse did *not* constitute a population genetic bottleneck, however, appears likely for several reasons. First, the genetically effective population size during the bottleneck would have had to have been very small, on the order of 10 or fewer individuals, in order to account for the current low level of heterozygosity (Chakraborty and Nei 1977). Second, sardine populations in southern Baja California and in the Gulf of California were unaffected by the collapse of the California fishery (Murphy 1969; Sokolov 1974), yet these populations today show low variation also. Finally, by analogy, the Japanese sardine, *Sardinops melanosticta*, which also experienced a severe fishery collapse in the 1940's but has since recovered (Kondo 1980), does not have reduced levels of genetic variation (Fujio and Kato 1979; Table 8).

Alternatively, a restriction in population size in the more distant past might explain low variation in the Pacific sardine. The historical record of scale deposits in varved, anaerobic marine sediments of the Santa Barbara Basin, southern California, does show that, relative to northern anchovy and Pacific hake, Pacific sardines were always less abundant and much more frequently absent (Soutar 1967; Soutar and Isaacs 1969, 1974). Over the past 1,850 years, the Pacific sardine was abundant during 12 periods, each lasting from 20 to 150 years. Intervals between these periods of abundance

[1]Parrish, R. H. 1983. Evidence for a fall spawning anchovy stock. Paper presented at 1983 CalCOFI Conference.

lasted, on average, 80 years and ranged in duration from 20 to 200 years (Soutar and Isaacs 1969). One or more of these periods of low abundance could have been a severe enough bottleneck to cause loss of variation, but this hypothesis may be difficult to falsify. According to Fitch (1969), fossil remains of *Sardinops* are absent from samples of California Pliocene and Pleistocene sediments, whereas evidence of five other pelagic species (*Clupea pallasi, Engraulis mordax, Merluccius productus, Scomber japonicus,* and *Trachurus symmetricus*) is present in at least some samples. This raises the possibility that *Sardinops sagax caerulea* may be a recent arrival in the California Current System and that the low variation is attributable to a small number of founders rather than to a subsequent bottleneck.

Other than such historical hypotheses, we can pose no ecological explanation of low genetic variation (such as provided for decapod crustaceans by Nelson and Hedgecock 1980, for example); the ecology of the Pacific sardine does not appear to be unique relative to those clupeoids having higher levels of variation (Blaxter and Hunter 1982). So we are left at present with no compelling hypothesis to explain the observation of low genetic variation in the Pacific sardine.

Structures of Historical and Contemporary Populations of the Pacific Sardine

Sprague and Vrooman (1962) and Vrooman (1964) described three genetically distinct subpopulations of *Sardinops sagax caerulea* on the basis of significantly different frequencies of a C-positive blood factor (13.6% in samples taken from California waters, 6.0% in samples taken from Baja California, and 16.8% in fish from the Gulf of California). Regrettably, though understandably, electrophoretic separation of allozymes has completely supplanted immunological methods for studying population structure. Data comparable in quantity and quality to historical data on serotype frequencies would be difficult to gather today. A considerable drawback to the immunological method is the requirement for fresh blood, whereas allozymes can be readily obtained from fresh or fresh frozen, muscle or visceral tissues. Moreover, allozyme methods allow a much larger survey of genes than does blood typing; this, in turn, provides for statistical analyses of genetic diversity that take into account the large component of variance among loci (Nei 1978).

Our finding of low genetic variation across a widespread sampling of Pacific sardines contradicts the hypothesis that there are currently genetically different, geographic subpopulations of Pacific sardine. Combined with the recency of the Pacific sardine's reexpansion into the California Current (Wolf et al. 1987), our observations support the alternative hypothesis that this species comprises a single, homogeneous gene pool. Examination of the distributions and abundances of sardine eggs and larvae (Ahlstrom 1954, 1957) does suggest the possibility of dispersal around the tip of Baja California, particularly during cold-water (anti-El Niño) years.[2] Our data on the sharing of rare alleles by widely separated populations support this conjecture by implying a high rate of gene flow throughout the range of the species (Slatkin 1985).

The present study does not falsify the subpopulation hypothesis for historical sardine populations, but our data show that it is unlikely. The former hypothesis requires that only a single southern subpopulation survived the fishery collapse to repopulate the Gulf of California, the Pacific coast of Baja California Sur, and more recently, the California Current. Data on the frequency of C-positive blood type in contemporary sardine populations would be useful. However, morphological and life history data also played an important role in past inferences concerning the structure of historical sardine populations (Radovich 1982). The implications of our data on morphological variation among contemporary populations are discussed next.

Morphological and Life History Variation Among Historical and Contemporary Pacific Sardine Populations

Life history traits, such as the schedules of age-specific growth, mortality, and reproduction, and the covariances among these traits, determine responses by fish populations to exploitation (Cushing 1973; Nelson and Soulé 1987). Indeed, the historical biology of the California sardine fishery and its demise provides an elegant example of this axiom. An important

[2]R. A. Schwartzlose, Centro de Investigaciones Biologicas de Baja California sur and Scripps Institution of Oceanography, La Jolla, CA 92093, pers. commun. 1988.

feature of the collapse of the sardine fishery was its north-to-south progression, which owed greatly to the interaction of underlying life history variation (in particular, steep north-south clines in size-at-age, age of first reproduction, maximum size, and the schedule of natural mortality), geographical shifts in fishing pressure, and natural between-year variation in recruitment (Murphy 1966; Radovich 1982). That life history variation was built upon genetic differences among geographic populations, however, now appears unlikely from the results of our study.

The single, most obvious component of morphological variation in Pacific sardines today is a geographic cline in size-at-age that is as steep and as large as that seen in historical populations (Fig. 2). In the past, such differences were used by several authors to infer the existence of genetically distinct subpopulations, yet the differences have been reestablished in genetically homogeneous, contemporary populations within just a few generations. This implies that rapid differentiation of growth rate among geographic populations—probably together with differentiation of correlated life history features such as age at first reproduction, maximum size, and age-specific mortality (Clark and Marr 1955; Blaxter and Hunter 1982)—is largely environmentally, and not genetically, determined. This is not to say that there are not genes that determine life history traits; but variation of these genes cannot be responsible for geographic variation in life history. The genotype of the Pacific sardine must instead provide for remarkable plasticity in life history phenotype.

One must now be skeptical of the interpretation that life history differences among historical sardine populations were conditioned by genetic differences among subpopulations or races. The question of which sardine stock is now recovering is moot. More importantly, it appears that information on the biology of sardine populations prior to the collapse of the fishery can safely be used for area-specific fisheries models of the recovering stocks.

ACKNOWLEDGMENTS

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Spawning and Survival Patterns of Larval Northern Anchovy, *Engraulis mordax*, in Contrasting Environments—A Site-Intensive Study

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ABSTRACT: During the 1985 spawning season of the northern anchovy, *Engraulis mordax* Girard, off southern California, a serial field study at contrasting sites linked measurable environmental characteristics with parameters of larval anchovy growth and survival and determined a range of environmental conditions over which northern anchovy had recently spawned. Surface and water column characteristics were measured while following surface drifters at each site, and their relation to corresponding measurements of larval anchovy production, growth, mortality, and starvation are reported.

The nearshore site was eutrophic with low current speeds, low wind speeds, and high forage levels which are characteristic of coastal spawning areas. The offshore site, by contrast, was relatively oligotrophic and had higher surface mixing rates, a deeper mixed layer, reduced stability in the pycnocline, and lower forage levels.

Among the measured characteristics of the ichthyoplankton, only one, the larval production rate, was markedly different at the two sites. Although habitat suitability for adult anchovies was different, survival probability for larval anchovies was more equivalent at the two sites than inspection of single parameters of the environment suggested. In contrast with the view that the northern anchovy spawns indiscriminately, the results of this study suggest that components of the adult northern anchovy population tend to spawn under conditions and at levels that yield consistent survival probabilities for their offspring.

Since Lasker's (1975, 1978, 1981) pioneering work on causes of larval fish mortality, recent developments have made techniques available to assess age-specific larval growth, mortality, and physiological condition. These developments have piqued interest in field studies that link environmental processes to survival probabilities for larvae of broadcast spawners. Here we present the results of a site-intensive shipboard study that combined newly available measures of larval condition with a suite of physical and biotic measures of their environment in the Lagrangian setting provided by near-surface drifters to determine local variations of a few days duration. Our results are intended to guide the design and execution of programs that address the recruitment process and its relation to the spawning environment.

Conditions under which northern anchovy, *Engraulis mordax* Girard, spawn and under which their eggs and larvae survive presently are known mainly from cruises of the CalCOFI program, which are quasi-synoptic surveys of broad areas of the spawning domain during which limited sets of environmental observations and measurements have been made (cf. Reid 1988). Owing to limits imposed by time and resources, such surveys do not yield knowledge of the local fate of spawned products because the methods that characterize survival likelihood of larval fish have only recently been developed and verified, and because local changes (those embedded in the surface flow) are not knowable by the survey approach.

METHODS

Site Selection

Criteria for selection of the two study sites were that each must 1) show evidence of recent spawning by anchovy, 2) contrast with the other site in macroscopic setting and environmental character, and 3) exhibit no local gradients indicative of smaller scale (0.1–10 km) environmental

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heterogeneity. The study followed a routine survey by the California Cooperative Fisheries Investigations (CalCOFI Cruise 8502) of the northern anchovy spawning domain. Visual inspection of plankton catches made on this survey yielded estimates of northern anchovy egg abundance at 4–10 nmi intervals. Within areas of high egg abundance, the ship's survey records of 3 m temperature and in vivo phytoplankton pigment fluorescence were scanned for evidence of local gradients. Low variations of pigments and temperature in the vicinity of possible sites were verified by inspection of available satellite images of sea surface temperature and surface layer color, and several sites were then targeted for this study.

At sea, we verified that our criteria held at each site by inspection of plankton tows to confirm recent (and therefore sustained) spawning activity, and by inspection of underway records for local homogeneity of temperature and pigment fluorescence at 3 m depth. We occupied sites shown in Figure 1.

Procedures on Site

Upon verification that a site met the three criteria, we launched a radio-transmitting surface drifter. The ship then moved several nmi to launch a second drifter. Thereafter, we alternated our station pattern between the two drifters, locating each drifter by radio direction-finding equipment and visually. Each site was thus defined, in the Lagrangian sense, to be the water corpus that was moving along with the two drifters. We assumed that both drifters at each site were implanted in macroscopically homogeneous water with respect to physical and biological character. We examine the limits of this assumption by contrasting variations within and between drifters at the same site.

Stations were patterned around each drifter, in turn, at cardinal points 2 km from the drifter. Vertical plankton tows, "CalVETs" (Smith et al. 1985), were made with 150 μm mesh nets from 50 m depth at all four stations to catch fish eggs and larvae to determine age-specific anchovy production and mortality. Oblique bongo tows were made to and from 50 m depth with 333 μm mesh nets and, after we lost the 333 μm mesh nets, with 505 μm mesh nets to catch northern anchovy larvae for estimation of starvation incidence and recent growth rate. At two of the four stations, paired vertical tows similar to CalVETs were made from 50 m depth with 75 μm mesh and 333 μm mesh nets to estimate composition and quantity of larval food rations and of other small plankton, respectively. CTD/Niskin casts were made to 100 m depth at one station, per drifter visit, to measure physical structure of the water column and to get water samples at 10 depths to determine concentrations of particulates, chlorophyll-a and phaeopigments. Secchi depth was determined at one station (daylight permitting) at each drifter to estimate thickness of the euphotic layer. Standard weather observations were made once per drifter visit.

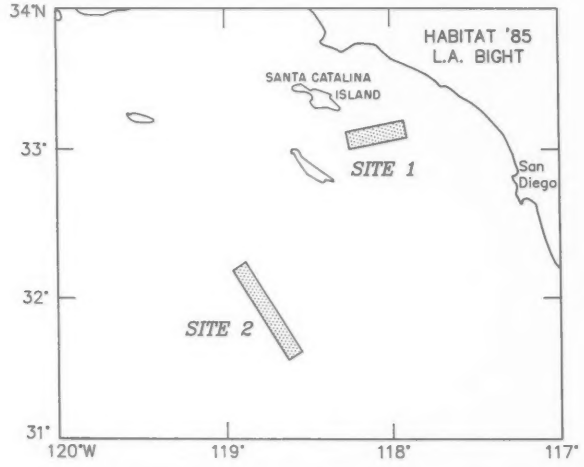


FIGURE 1.—Study site locations in the Southern California Bight.

Environmental Characteristics

Surface Drift

Drifter positions were determined by a combination of satellite navigation, Loran-C, and Decca radar over the course of the study, and were precise within 0.1 km. The drifters were designed as described by Davis et al. (1982) to minimize the effects of wave motion and of wind drag on exposed surfaces, both of which cause deviations of drifter motion from that of water parcels. The 2 km station spacing around each drifter was large compared with precision of drifter position and with deviation of the drifter's motion from surrounding water motion.

Vertical Temperature and Salinity Profiles

Temperature, conductivity, and pressure were recorded with a Neil Brown CTD, following methods used by NOAA/Southwest Fisheries Center.[1] Briefly, 0.25 s scans of temperature, conductivity, and pressure were recorded as the CTD profiled at 20–40 m/min. Conductivity and temperature records corrected for temperature lags are smoothed by a 5–point weighted running mean with binomial coefficients of 1, 4, 6, 4, 1. Salinity was computed using the Practical Salinity Scale of 1978. Salinities and temperature were compared and justified with salinity and temperature values from a hydrographic bottle tripped in the near-surface layer during each cast. Final data were enumerated at 2 m depth intervals.

Phytoplankton Pigments

Chlorophyll-a and phaeopigment-a concentrations were determined from fluorescence readings on a Turner 111[2] Fluorometer before and after acidification of 24 h extractions in 90% aqueous acetone of material retained on Whatman GF/C glass filters after filtration of 140 mL water samples.

Particles

Particle concentration and size distribution (16–160 μm equivalent diameters) were determined with a Coulter model Ta counter with a 280 μm pore configured to count particles in a 20–200 mL sample volume. Counts usually exceeded 40,000 per sample. These determinations stopped part way through the study owing to equipment malfunction at the second site.

Microplankton

Microplankton samples were aliquoted prior to counting. A 0.5 mL Stempel pipette was used 10–40 times to withdraw a subsample from the well-stirred original sample after adjusting the original volume to 750 mL. When 10 Stempel subsamples yielded too many plankters to enumerate, the sample was divided with a Folsom splitter to yield a countable fraction from at least 10 Stempel subsamplings.

Microplankton samples were enumerated in covered chambers with a Wild dissection microscope (at 250 magnification) to determine mean concentrations of larval anchovy food organisms in the upper 50 m. Food organisms are here assumed to be those having ingestible dimensions (20–160 μm width), no pronounced spines or processes that would interfere with ingestion or with gut wall integrity, and, except for ingestible eggs, some degree of motility (Rojas de Mendiola 1974; Arthur 1976). Food concentrations and rations given here are underestimated because larvae are known to take organisms smaller than were retained by the meshes of the 75 μm mesh net used (Rojas de Mendiola 1974; Arthur 1976). The sampled food fraction probably represents the major part of available food rations; although less in number, this fraction is greater in volume than the unfiltered fraction and is captured selectively by larvae (Lasker and Zweifel 1978; Theilacker and Dorsey 1980). The food retained by the net is assumed here to be the majority of, and proportional to, the total rations available to larvae over the 50 m layer sampled.

Zooplankton

Zooplankton counts were made on all organisms collected in the 333 μm mesh vertical tows. Samples were not aliquoted. The net tow method used precluded quantitative representation of faster or rarer organisms, including some types of potential predators on fish larvae. Determined for each sample were number of species, number of specimens of each species, and sex ratios (where applicable) for the following major tax-

[1]K. Bliss, Oceanographer, Southwest Fisheries Center, La Jolla, CA, 92038, pers. commun. May 1985.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

onomic groups: Medusae, Siphonophorae, Ctenophora, Chaetognatha, Cladocera, Ostracoda, Amphipoda, Copepoda, Euphausiidae, crustacean larvae, other invertebrate larvae, pelagic Mollusca, Polychaeta, Tunicata, Radiolaria, and Foraminifera. Anchovy eggs and larvae, sized to the nearest 0.25 mm, were also enumerated from these collections. Zooplankton enumerations are given in detail in Alvariño and Kimbrell (1987).

Larval Characteristics

Larval Growth

Growth of larvae was estimated from 224 larvae collected in 15 tows at Site 1 and from 116 larvae collected in 30 tows at Site 2. Samples for otolith ageing of larval anchovies were taken from the portside net of bongo tows and were preserved after removal of gelatinous zooplankters in 80% ethanol buffered with 20 mM tris [hydroxymethyl] aminomethane. Larvae were sorted from the plankton and stored in the same preservative.

Standard lengths of larvae were measured prior to removal of their otoliths. Preserved standard lengths were converted to live lengths using a correction factor for net shrinkage (Theilacker 1980). At Site 1, tow duration was six minutes and each sample was fixed within five minutes of tow completion. Length of the inshore larvae were corrected by a net shrinkage factor of eight minutes. Tow duration at Site 2 was also six minutes, but because of the large number of salps collected offshore, time before preservation increased to about 10 minutes. Lengths of offshore larvae were corrected for 13 minutes of net shrinkage.

Daily increments in the otoliths were counted using a compound microscope equipped with a closed-circuit television system, a video coordinate digitizer, and a microcomputer (Methot and Kramer 1979). Age from hatching was determined from the number of daily rings in the otoliths. Because the initial ring is deposited at the time of first feeding, at about five days from hatching, time since hatching is 5 days more than the ring count (Brothers et al. 1976).

Laird-Gompertz growth curves were fit to the length at age using nonlinear regression. To compare differences in growth rates between the two sites, analysis of covariance was performed on segments of the data so that the assumption of linearity was reasonable.

Larval Production and Mortality

Age-specific larval anchovy production rates were computed from counts of larvae in 1 mm size classes to 9 mm preserved standard length (SL) from bongo tows and in 0.5 mm size classes to 7 mm SL from CalVETs. Counts of larvae were corrected for volume of water filtered, for net avoidance, and for losses owing to extrusion through the net meshes (Zweifel and Smith 1981). Larval production at each age was estimated by dividing size-specific larval abundance by time spent at each size. Duration at size was specfied from Laird-Gompertz growth curves (Methot and Hewitt 1980; Lo 1983).

Larval mortality curves were based on the Pareto decay function (Lo 1985):

$$z(t) = \beta/t$$

where $z(t)$ is the instantaneous mortality rate (IMR), β is the IMR coefficient, and t is age (days) since spawning. Daily production is given by

$$P_t = P_0(t/t_0)^{-\beta} \quad t_0 < t < 20\ d$$

where P_t is daily larval production at age t, P_0 is initial larval production (at hatching), t_0 is age at hatching, specified from hatching time as a function of incubation temperature (Lo 1983). Thus, as larvae grow older, the rate at which they appear in the next age group is diminished by the factor given by β.

The above equation (referred to subsequently as the nonlinear model) can be expressed in linear form by taking the natural logarithm of both sides:

$$\ln(P_t) = \ln(P_0) - \beta \ln(t/t_0)\ .$$

Both the nonlinear and the log-linear regression models can be used to estimate parameters P_0 and the IMR coefficient β. The log-linear equation is mainly used in this study to compare β between sites.

Production and mortality of anchovy larvae at Site 1 were estimated from 48 bongo samples (20 using 333 μm mesh nets and 28 using 505 μm mesh nets) and from 49 CalVETs using 150 μm mesh nets. At Site 2, these parameters were estimated from 49 bongo samples using 505 μm mesh nets and from 50 CalVETs using 150 μm mesh nets.

Larval Condition

Starvation incidence was estimated from histological criteria on 141 anchovy larvae from Site 1 and on 119 larvae from Site 2. The larvae were collected with nonquantitative bongo nets towed to 50 m. Although the best preservation procedure for histological samples is to preserve larval fish in Bouin's fixative within 3 minutes after capture, 5–6 minutes were required to obtain representative samples to 50 m. After fixing in Bouin's fluid for 24–48 hours, samples were transferred to 70% ethyl alcohol for storage.

The nutritional state of northern anchovy larvae is usually classified by grading the appearance of tissues of the brain, cartilage, notochord, liver, pancreas, and gut (O'Connell 1976). But because many of these tissues had lysed owing to extended time before preservation, an additional criterion was used in this study. This criterion, the height of midgut mucosal cells, was unaffected by the 5–6 minutes needed to fix the larvae (Theilacker and Watanabe 1989). Heights of midgut mucosal cells were divided into three categories (healthy, intermediate, and starved) according to laboratory results (Theilacker and Watanabe 1989). As northern anchovy develop past 6 mm SL, the midgut folds to increase the absorptive area. The fold makes it difficult to measure cell heights of larger larvae. To apply the durations determined for the laboratory fish to the field samples, the size of the field-collected larvae was adjusted to equal the size of preserved laboratory fish of known feeding history (Theilacker 1980). Details of these manipulations are given in Theilacker and Watanabe (1989).

RESULTS

Environmental Variations Within and Between Drifters and Sites

Surface Drift

Drifters were tracked as shown in Figure 2. Released 10 nmi apart at Site 1, Drifters A and B moved generally eastward, away from Santa Catalina Island, on slightly convergent courses. Mean speeds over their 2.7 days at sea were 17.1 cm/s and 18.7 cm/s (about 15.5 km/dy). Range of speeds measured by drifter displacements over 8 h intervals were 5.6–34.7 cm/s and 6.8–32.9 cm/s.

Released 5 nmi apart at Site 2, Drifters A and B moved in a southeast-trending arc, again on slightly convergent courses. Mean speeds over their 2.5 days at sea were 34.6 cm/s and 37.4 cm/s (about 30 km/d), twice as fast as at Site 1. Speed ranges measured were 15.3 cm/s to 45.4

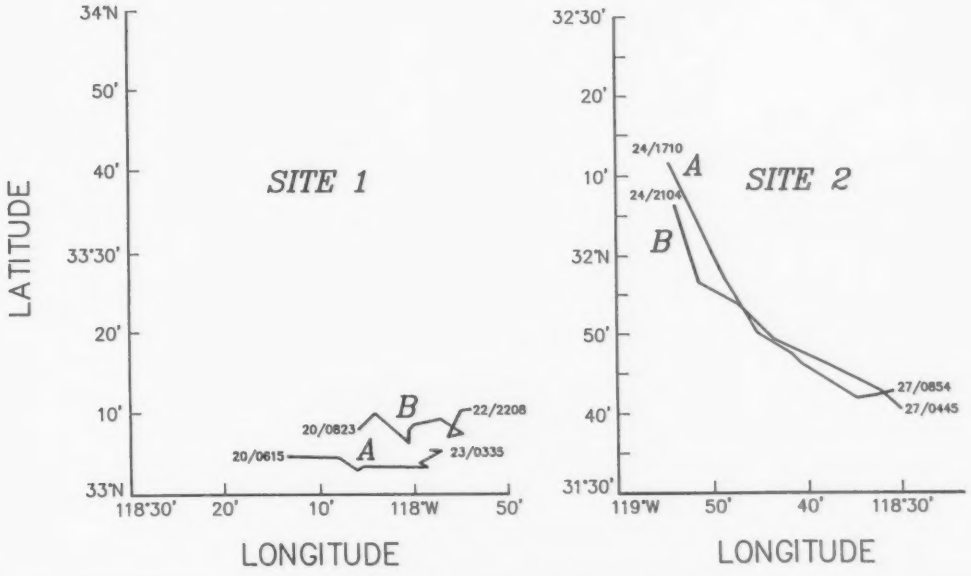
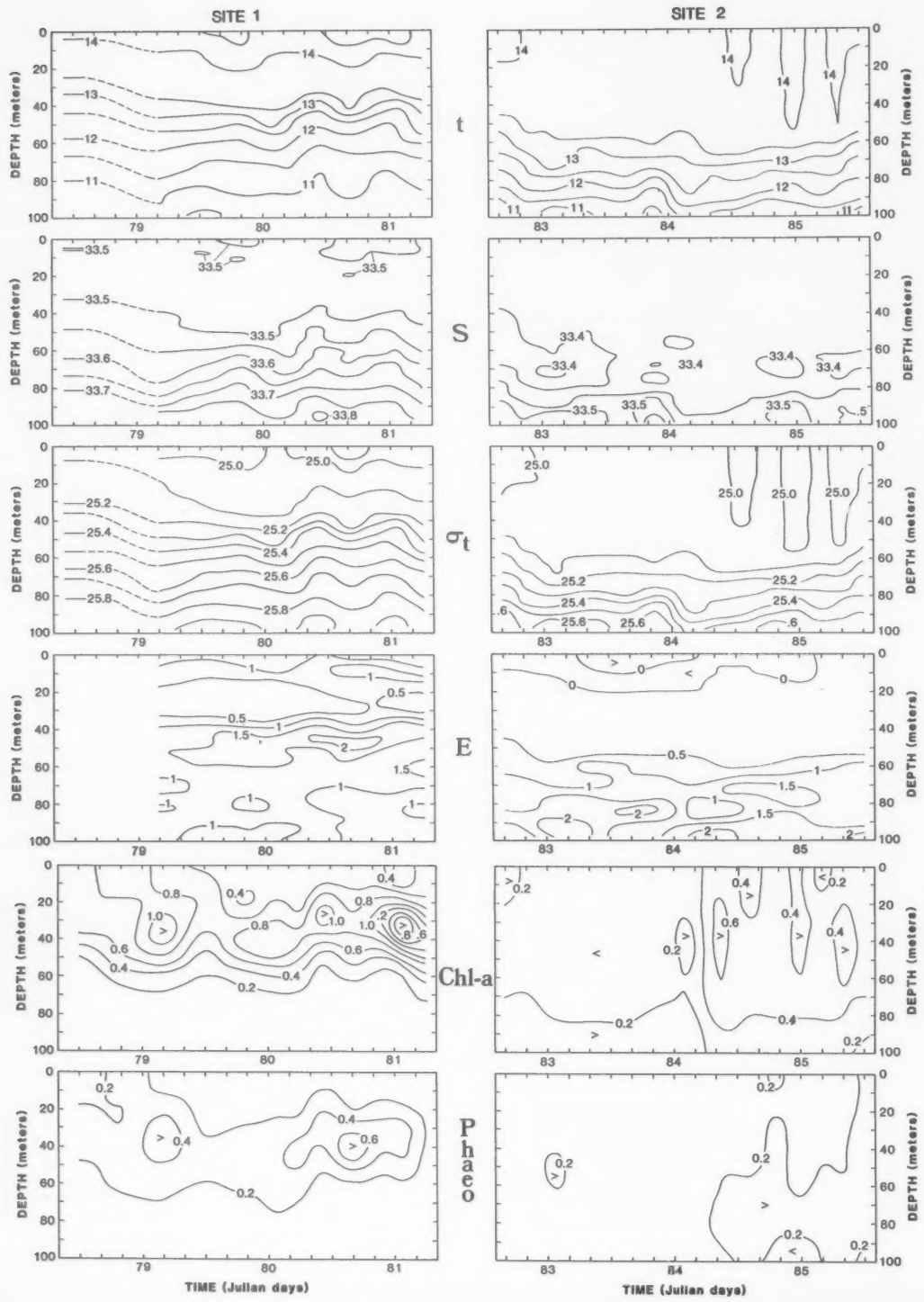


FIGURE 2.—Drifter trajectories along *Sites 1* and *2*.


SITE 1
SITE 2
t
S
σt
E
Chl-a
Phaeo
DEPTH (meters)
TIME (Julian days)

cm/s and 18.8 cm/s to 48.2 cm/s. Drift direction at Site 2, predominantly longshore, indicated that Site 2 larvae had been spawned offshore rather than drifting out from an onshore spawning area.

The degree to which drifter displacements paralleled one another at each site (Fig. 2) indicated homogeneous, nondivergent flow of the surface layer and general integrity of each water corpus being investigated. Similar rates of separation of drifter pairs indicated no differences between rates of lateral diffusion between sites.

Vertical Structure

Physical structure of the upper 100 m at both sites exhibited no overall trends for the duration of the study (Fig. 3). Variations of isopleth depths in the pycnocline at Site 1 were greater during the second half of the period, perhaps owing to increased internal wave activity.

A slight warming trend over the course of the studies was indicated by increased surface layer temperatures at both sites. The trend was likely due to local heating of the mixed layer. Heat content of the upper layer increased at Site 2 but no trend was detected at Site 1.

Local diurnal heating was apparent at Site 1 from continuous temperature records at 3 m depth as well as from CTD casts. Higher winds and a thicker mixed layer at Site 2 obscured diurnal temperature variations.

Vertical sections of phytopigments (Fig. 3) gives a less conservative picture of variations. Intensification of the maximum chlorophyll and phaeopigment layers over the course of studies occurred at both sites. In view of the lack of change of temperature, salinity, and density structure, the increase in pigment concentration was likely due to local processes rather than to advective processes. The change thus expressed the net product of primary production and grazing.

Composite T-S diagrams (Fig. 4), constructed from CTD cast data at each site, indicate that the drifters were set into waters of different structure and composition at the two sites. Site 2 water, closer in character to California Current core water (Lynn and Simpson in press), was cooler and less saline than Site 1 water. Site 1 water was likely derived from a mix of California Current core water (from the north, offshore) and coastal countercurrent water (from the south, nearshore), further modified by local warming of the surface layers in transit.

Plankton Quantity and Composition

Within sites, no major differences were apparent in plankton quantity or community composition along drifter paths. Over twice as many plankton organisms were caught by 333 μm mesh nets at Site 1 than at Site 2, and predatory copepods were 5 times more numerous at Site 1 than at Site 2 (Table 1). Plankton diversity was somewhat higher at Site 1 than at Site 2: on average, Site 1 tows yielded 144 invertebrate species, whereas Site 2 tows yielded 130 species. Perhaps the most striking difference in the zooplankton was the high abundance of salps at Site 2. No direct interactions are known between fish larvae and salps.

In terms both of rations and numbers, over twice as much larval anchovy food was caught by 75 μm mesh nets at Site 1 than at Site 2 (Table 1).

Summary

To compare habitats at the two sites, Table 1

[3]Lynn, R. J., and J. Simpson. 1989. The influence of bathymetry upon the flow of the undercurrent off Southern California. Unpubl. manuscr.

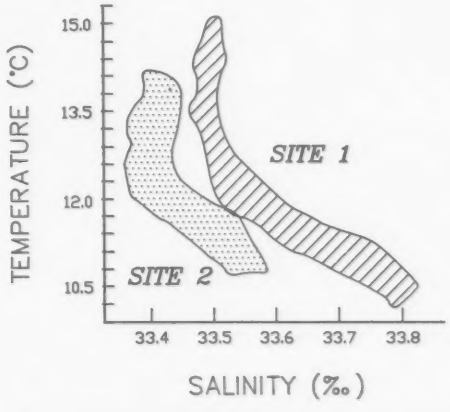


FIGURE 4.—Composite T-S diagrams at *Sites 1* and *2*.

FIGURE 3.—Vertical time sections of temperature (t), salinity (‰), density (σ_t), and stability (E) at Sites 1 and 2. Vertical time sections of chlorophyll-a and phaeopigment at Sites 1 and 2.

TABLE 1.—Comparisons between study sites—means (and standard deviations) of environmental characteristics at Sites 1 and 2. *n* is number of observations. Integrations are to 50 m depth.

	Site 1		Site 2	
	mean (SD)	*n*	mean (SD)	*n*
mixed layer depth (m)	37.6 (5.0)	11	57.7 (6.8)	14
wind speed (m/s)	3.27 (1.54)	15	8.97 (2.36)	14
stability max. ($E \times 10^7$)	4.00 (1.54)	11	3.47 (1.59)	14
depth of stability max. (m)	45.6 (7.8)	11	67.6 (8.7)	14
surface current speed (cm/s)	18.9 (10.2)	16	35.4 (10.4)	16
surface temp. (C)	14.50 (0.41)	50	14.04 (0.14)	50
surface salinity ‰	33.50 (0.011)	11	33.42 (0.044)	14
surface chlorophyll a conc. (μg/L)	0.56 (0.20)	11	0.37 (0.15)	12
surface phaeopigment conc. (μg/L)	0.14 (0.13)	11	0.10 (0.09)	12
integrated chlorophyll a conc. (mg/m^2)	45.3 (9.74)	11	33.8 (12.72)	12
integrated phaeopigment conc. (mg/m^2)	20.3 (4.77)	11	15.9 (7.64)	12
Integrated particle conc., 16–160 μm (no/cm^2)	44012 (44761)	11	66980 (67027)	5
Integrated particle conc., 50–160 μm (no/cm^2)	5854 (9405)	11	2607 (1138)	5
Secchi depth (m)	11.5 (2.0)	9	18.1 (2.7)	8
food conc. >75 μm (no/L)	31.4 (13.9)	26	13.5 (12.0)	24
food conc. >75 μm ($\mu m^3/L$)	19.6 (5.7)	26	8.1 (7.0)	24
zooplankton conc. (no/m^3)	625 (216)	26	236 (160)	24
predatory copepods (no/m^3)	121 (79)	26	24 (32)	24
zooplankton spp. (species/tow)	144	26	130	24
copepod spp. (species/tow)	65	26	60	24

gives means and variations among environmental parameters of energy input and dissipation, responses of the plankton communities, and levels of food supply and predation pressure to which the larvae were exposed. Analyses of variance of environmental characteristics demonstrated much smaller variations between drifters within sites than between sites.

In review, changes over study periods at both sites were local, not advective; we resampled the same water and larval population within sites. Vertical gradients were shoaler and more intense at Site 1. Temperature and salinity relations in the upper 100 m indicate different recent histories of the waters at the two sites. Surface layers at Site 1 were warmer, more saline, less turbulent, less transparent, and contained higher concentrations of larval foods and other

plankton. Plankton community structure was different between sites: most notably, predatory copepods were more abundant at Site 1 and salps were more abundant at Site 2.

Larval Parameter Variations Within and Between Drifters and Sites

Larval Growth Rates:

Ranges of size and age of larvae differed between sites. Site 2 samples included larvae that were larger (and older) than those at Site 1. The average age of larvae was 6.9 and 11.5 days from hatching at Sites 1 and 2, respectively. Larval length averaged 7.8 mm and 9.0 mm at Sites 1 and 2, respectively. Thus the offshore Site 2 was inhabited by older and slightly longer larvae than Site 1. Offshore drift of larvae hatched inshore into the region of Site 2 (Smith 1972) may account for this phenomenon, as may higher predation on older larvae at Site 1. The latter explanation is favored because the observed flow patterns (Fig. 2) do not suggest that larvae were transported offshore from nearshore areas.

To assess the growth of larvae in these two stations, the Laird-Gompertz model was used to fit the length-age data:

$$L_t = L_\infty(L_0/L_\infty)^{\exp[-\alpha t]}$$

where t is time since first feeding at 5 days after hatching, L_0 is larval length at first feeding, and L_∞ is the asymptotic length. The maximum and minimum fish lengths in the sample have strong influence on the length parameter estimates (L_0 and L_∞) and on the growth coefficient (α). The resulting growth coefficients at the two sites (Table 2) are 0.1 for the inshore station and 0.05 for the offshore station. A standard growth coefficient of 0.05 is used by CalCOFI (Methot and Hewitt 1980).

We compared total growth rates of fish younger than 18 days (after hatching) at the two sites, assuming a linear growth rate to be reasonable because of difficulties in comparing differences between nonlinear curves. Larvae at the offshore Site 2 had a larger asymptotic length and a lower growth coefficient than at the inshore site. The null hypothesis, that growth was equal at the two sites, was tested using analysis of covariance. When the test was performed on lengths uncorrected for shrinkage or on lengths corrected for the same shrinkage, the slopes at the two sites were not significantly different but the mean lengths were. (A true difference between mean lengths would indicate that anchovy larvae had hatched at a larger size at Site 1 than at Site 2, or that Site 2 larvae underwent starvation at the first-feeding stage and then recovered.) However, when larval lengths from Site 2 were corrected for greater handling time, then neither the slopes nor the adjusted lengths differed significantly between the two sites (Table 3). In short, corrected data indicate that no difference existed in larval growth between the sites.

Larval Production and Mortality Rates

Larval production at age (larvae <20 days from spawning) was used to model larval mortality. For mortality analysis, age is defined as time since spawning. Larval production was computed as described above in Methods, and larval age was derived from live size using a Gompertz growth curve. Three growth curves were available for computing larval age: the standard growth curve used for routine annual anchovy larval assessment, and two site-specific growth curves constructed from length-age data collected at each of our sites. We elected to use the standard growth curve to convert larval size to age for both sites because no significant difference in total growth rates for larvae <20 days since spawning was detected between two site-specific growth curves, and because the growth coefficients estimated from two sites were also similar to that of the standard growth model (all equal to 0.05) when the maximum and minimum lengths of larvae were set to be 27 mm and 4.1 mm, corresponding to the standard growth curve. Both nonlinear and log-linear regression

TABLE 2.—Parameters of Laird-Gompertz growth curves for northern anchovy larvae at Site 1 and Site 2. L_0 is larval length at first feeding; L_∞ is the asymptotic length; and α is the growth coefficient. Lengths are corrected for differential handling times.

Parameter	Site 1	Site 2	CalCOFI
L_∞ (mm)	14.7 (0.6)	20.5 (1.8)	27
L_0 (mm)	4.9 (0.1)	5.2 (0.2)	4.1
α	0.10 (0.01)	0.05 (0.01)	0.05
n	234	141	—
With L_∞ (mm) fixed at 27 mm and L_0 (mm) fixed at 4.1 mm,			
α	0.05 (0.001)	0.05 (0.01)	

TABLE 3.—Comparison of growth rates of northern anchovy larvae between Site 1 and Site 2 for post-yolk-sac larvae less than 18 days old, using analysis of covariance.

Linear regression of growth. L is length, t is time since hatching, and n = total number of larvae sampled.

Site 1 $L_t = 7.33 + 0.46\ (t - 9.99)$ $n = 197$
Site 2 $L_t = 7.82 + 0.46\ (t - 11.54)$ $n = 79$

Analysis of covariance between sites

Source of variation	df	Sum of squares	Mean squares	F	Prob. (tail)
Equality of adjusted means	1	2.57	2.57	3.23	0.07
Zero slopes					
All covariates	1	709.76	709.76	892.98	0.00
error	273	216.99	0.79		
Equality of slopes all covariates and all groups	1	0.02	0.02	0.02	0.89
error	272	216.97	0.80		

were used to estimate the larval production at hatching (P_0) and mortality coefficient (β).

Mortality Estimates

Data in three arrays were used to estimate mortality: bongo larvae alone, bongo larvae plus 2.5–4.0 mm larvae from CalVETs, and bongo larvae plus 3.0–4.0 mm larvae from CalVETs (Tables 4, 5). The nonlinear regression gave estimates of β ranging from 1.15 to 2.18 (equivalent to IMR of 0.115–0.218 for larvae of age 10 days) for Site 1 and 1.06–3.03 for Site 2. The lower values of β were caused by low numbers of 2.5 mm larvae in CalVET samples. The log-linear regression produced more consistent estimates of β than those from nonlinear regression: Site 1 values ranged from 3.32 to 3.94 and Site 2 values ranged from 2.87 to 3.47. Estimates of P_0 at hatching age ranged at Site 1 from 12.03 to 28.38, and for Site 2 from 1.37 to 4.23. For all data arrays, site differences in larval production rates were apparent (Tables 4, 5), but site differences in mortality rates were not (Table 6).

Comparison of Larval Production and Mortality Coefficients Between Sites

Larval samples from bongo tows were used to compare the mortality between sites. Analysis of covariance was performed on the logarithmic transformation of age and larval production. The results of the analysis indicated that the site difference between mortality coefficients was not statistically detectable whereas site difference between larval production rates was (Table 6).

We also compared the larval production and mortality at the two sites (Table 5) with those over the northern anchovy spawning domain as sampled by the CalCOFI 8502 survey ($P_0 = 4.81$ with SE = 0.30, and $\beta = 2.21$ with SE = 0.11 for 37 positive CalVET tows out of 45). Larval production at Site 1 was much higher than the average over the CalCOFI 8502 survey region, but production at Site 2 and larval mortality at both sites were similar to the survey region averages.

Figure 5 shows the larval production-at-age curves at the two sites and, for comparison, larval production curves for anchovy spawning domains as sampled on CalCOFI Cruise 8502, just prior to our site-intensive program. Site 1 displayed high production of all larval ages, which was higher than its subdomain (CalCOFI Region 7), whereas Site 2 production was somewhat above that of its subdomain (CalCOFI Region 8) and somewhat below that of the entire spawning domain as sampled ("all regions").

Starvation Incidence

Midgut cell height is the histological criterion of larval feeding history. The range of cell height and the cell height change with larval size were similar at both sites (Fig. 6). The similarity

TABLE 4.—Northern anchovy larval production per unit area per day at age at Sites 1 and 2 from bongo and CalVET nets, based upon "regular" growth. *n* is total number of tows, pos. *n* is number of tows with larvae.

	Site 1		Site 2	
Capture size (mm)	Average age (d)	Production no./0.05 m^2/d	Average age (d)	Production no./0.05 m^2/d
Bongo net				
2.5	4.72	10.67	5.29	0.95
3.75	8.30	5.57	9.20	0.19
4.75	11.04	0.54	11.91	0.074
5.75	13.44	0.16	14.38	0.033
6.75	15.64	0.096	16.69	0.024
7.75	17.78	0.085	18.86	0.022
8.75	19.84	0.095	21.06	0.016
n(pos.*n*)	48 (48)		49 (46)	
CalVET net				
2.5	3.60	6.44	3.81	0.674
3.0	5.09	7.81	5.37	1.221
3.5	7.16	7.65	7.56	1.503
4.0	8.90	3.19	9.27	0.445
4.5	10.10	0.27	10.50	0.098
5.0	11.41	0.44	—	—
5.5	12.86	0.04	—	—
6.0	13.38	0.04	—	—
6.5	14.78	0.02	—	—
n(pos.*n*)	49(49)		50(40)	
temperature	14.25C		14.05C	
hatching age	3.05d		3.23d	

[1]Production computed from total number of tows(n).

TABLE 5.—Estimated northern anchovy larval production at hatching (P_0) and mortality coefficient (β) from nonlinear and log-linear regression for Sites 1 and 2 using various data sets and "regular" growth parameter estimates.

	Site 1			Site 2		
Data sets	P_0 (SE)	β (SE)	MSE	P_0 (SE)	β (SE)	MSE
Nonlinear bongo only	28.38 (7.70)	2.18 (0.47)	1.78	4.23 (0.15)	3.03 (0.07)	0.0008
CalVET (2.5–4.0 mm) and bongo	12.03 (2.98)	1.15 (0.38)	6.01	1.37 (0.51)	1.06 (0.52)	0.1816
CalVET (3.0–4.0 mm) and bongo	23.79 (5.86)	1.85 (0.38)	2.47	2.99 (1.40)	1.80 (0.68)	0.1238
Log-linear bongo only	4.49 (0.77)	3.9 (0.54)	0.43	1.41 (0.22)	3.05 (0.15)	0.03
CalVET (2.5–4.0 mm) and bongo	3.79 (0.59)	3.32 (0.48)	0.74	1.36 (0.52)	2.87 (0.42)	0.57
CalVET (3.0–4.0 mm) and bongo	4.67 (0.58)	3.94 (0.45)	0.46	2.22 (0.49)	3.47 (0.38)	0.31

suggests that both larval populations had experienced comparable feeding conditions.

Although average daily mortality rates due to starvation of first-feeding anchovy larvae were higher at Site 1, 24%/d, than at Site 2, 12%/d (Table 7), the difference between sites was not statistically significant ($\chi^2 = 2.26$; $P > 0.15$). Incidence of starvation was low or nil after the first-feeding stage at both sites.

TABLE 6.—Comparison of mortality coefficients (β) of northern anchovy larvae (<20 days) between Site 1 and Site 2, using analysis of covariance. P_t is the larval production at age t; t is age (d) from fertilization. The values 3.05 and 3.23 are ages at hatching.

Log-linear regressions of mortality are

Site 1 $\ln(P_t) = 4.49 - 3.90\ [(\ln(t/3.05))]$

Site 2 $\ln(P_t) = 1.4 - 3.05\ [(\ln(t/3.23))]$

Analysis of covariance between sites

Source of variation	df	Sum of squares	Mean square	F	Prob. (tail)
Equality of adjusted means	1	13.26	13.26	50.90	0.00
Zero slopes					
All covariates	1	35.12	35.12	134.80	0.00
error	11	2.87	0.26		
Equality of slopes all covariates and all groups	1	0.52	0.52	2.24	0.17
error	10	2.34	0.23		

DISCUSSION

We had expected to find higher rates of larval northern anchovy growth and survival in the inshore than in the offshore environment. Bias or low precision cannot explain the similarity of growth and mortality coefficients between sites. The larval anchovy parameters might have been biased had we sampled larval populations imported from other sources by advection or diffusion over the course of the measurement periods, but our time series of environmental characteristics display no shifts to indicate short-term change of properties or of populations at the drifters. Similarly, lack of precision cannot be invoked: the number of tows and larvae were sufficient to distinguish mortality coefficients (β) differing by 0.5 with an 86% probability (Lo et al. 1989). We must accept that the mortality coefficients were and that many more similar tows would be necessary to distinguish between them.

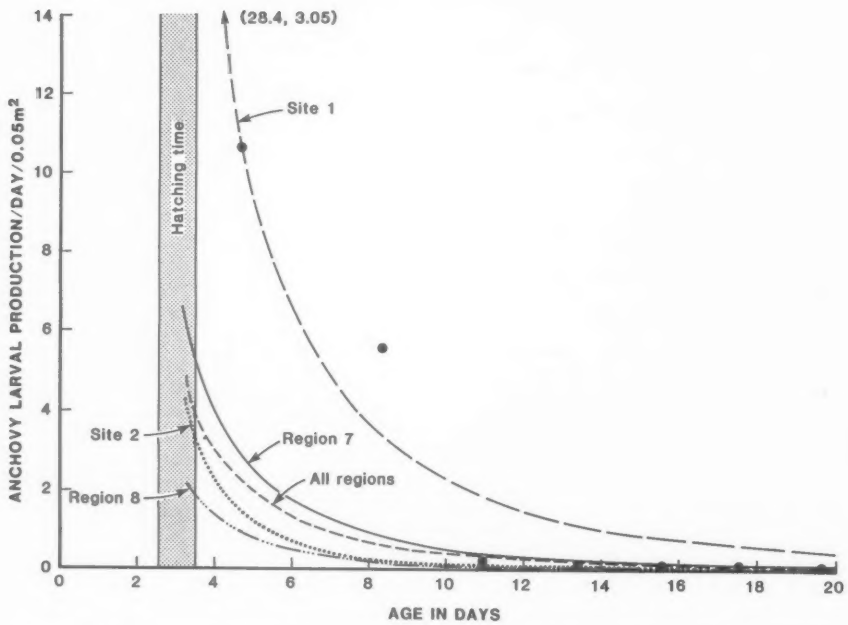


FIGURE 5.—Daily larval production vs. age for northern anchovy and fitted larval mortality curves for Site 1 and Site 2, and for CalCOFI 8502 survey and subregions. Points are for Site 1 only.

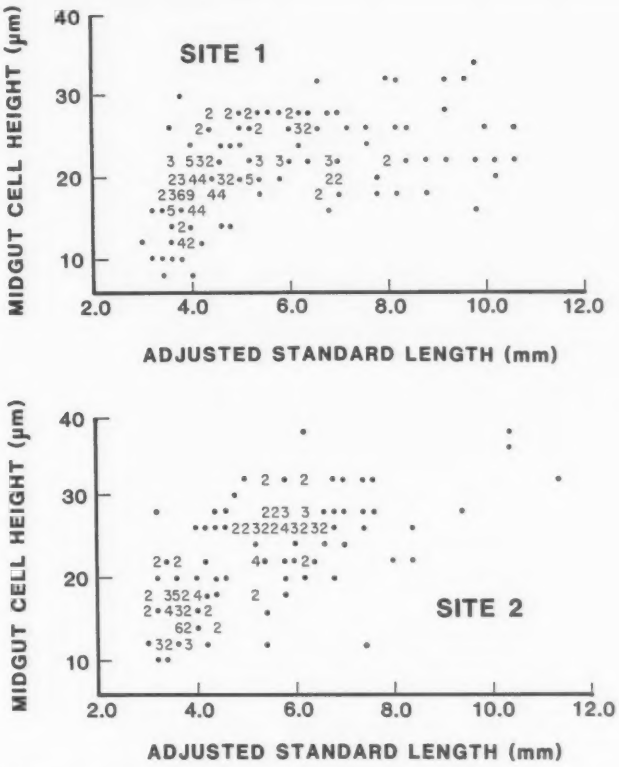


FIGURE 6.—Midgut cell heights of individual northern anchovy larvae collected at Site 1 (inshore) and at Site 2 (offshore).

TABLE 7.—Histological condition of larval northern anchovy at Sites 1 and 2. *n* = number examined; dur = duration; *n*/d = number/day; S = starved; I = intermediate; H = healthy; %/d = % dying/day due to starvation.

	Site 1					Site 2				
	S	I	H	total	%/d	S	I	H	total	%/d
3–4 mm (SL)										
n	9	17	28	54		4	32	21	57	5
dur	2	5	2.5			2	5	2.5		
n/d	4.5	3.4	11.2	19.1	24	2.0	6.4	8.4	16.8	12
4–5 mm (SL)										
n	1	11	48	60		0	5	20	25	
dur	2	3	2.5			3	3	2.5		
n/d	0.3	3.6	19.2	23.1	1	0	1.7	8	9.7	0
5–6 mm (SL)										
n	0	0	27	27	0	0	2	35	37	0
Total number examined				141					119	

Similarity of growth and starvation indices at the two sites indicates that most larvae had encountered sufficient forage to sustain "normal" growth rates, or that the fraction that had not done so were quickly removed from the system, i.e., not represented in our collections. Food abundance estimated from integrative tows may not reflect the actual availability of food to larvae because microplankton prey frequently occur in patches and laminae of very small extent (cf. Owen 1989). Also, larvae may have been sustained on food that passed through the net. Fewer larvae were collected at Site 2 than at Site 1, but starvation incidence was at least as low there as at Site 1. Furthermore, Site 2 larvae were growing as fast as those at Site 1, even though average microplankton concentration at Site 2 was less than half that at Site 1. Despite lower average food concentrations, there were zones at Site 2 that evidently contained enough food to support growth of the larvae.

An analogous result is given by Butler (1989), which showed that periods of diminished forage production, such as el Niño, have no discernible effect on growth rates of field-caught larvae. But Theilacker and Watanabe (1989) showed by experiment that starvation measurably retards larval growth. This apparent paradox is resolved if, in the sea, larvae that survive to be sampled have found enough food to grow at normal rates even in abnormal periods, whereas larvae that have been deprived to the extent that their growth is adversely affected soon vanish, perhaps by predation owing to their weakened condition rather than by starvation directly.

In contrast with the common view that northern anchovies broadcast sex products indiscriminately with the strategy that some get lucky, we advance the hypotheses that anchovy spawn where their offspring are equally likely to survive, even under widely different environmental conditions, and that these conditions mediate their spawning intensity. This is the central theme of MacCall's (1983) "Basin Model" of habitat selection by the northern anchovy.

The Basin Model postulates that when a population is large, its adults occupy less suitable habitats in which mortality of spawn per capita tends to equal that in more favorable habitats. This occurs because cannibalism of spawn by adults is higher in favored habitats than in peripheral habitats.

We roughly partition sources of overall larval mortality (β_t) into that due to cannibalism (β_c) and that due to other causes (other predation, β_p, and starvation, β_s). Diffusive change, a source of "apparent" mortality, is assumed from physical arguments above to be the same at both sites. Thus,

$$\beta_t = \beta_c + \beta_p + \beta_s .$$

If higher egg concentration denotes higher adult occupation, β_c was greater at Site 1 than at Site 2. Anchovy egg concentration at Site 1 averaged 37/m^3, 15 times the egg concentration at Site 2. This difference is too great to be attributed to differences in batch fecundity of the spawners, which varies by a factor of about two (Hunter et al. 1985).

For larval mortality, β_t, to have been equivalent at the two sites, mortality from other sources ($\beta_p + \beta_s$) is required to have been greater at Site 2 than at Site 1 to the degree of offsetting the difference between sites in parental consumption of spawn (β_c). But neither larval growth rates nor starvation incidence differed between sites, showing that their β_s values were about equal. This being so, cannibalism was offset by other predation rather than by starvation. This requires increased predation (β_p) at Site 2 over that at Site 1.

For comparison of β_p between sites, we formed rough indices of predation pressure, P, from catches by vertical net tow pairs. P is the concentration of the five most numerous predators caught by the 333 μm mesh net, divided by concentration of anchovy eggs and larvae caught in the corresponding 150 μm mesh net. Predator populations in the samples consisted mainly of raptorial copepods and chaetognaths. Mean values of P were 2.8 predators/anchovy at Site 1 (26 tows) and 5.5 predators/anchovy at Site 2 (24 tows). This difference indicates compensatory predation at Site 2. Confirmation of compensatory predation, however, is not possible from this data set because our nets missed larger, faster predators such as euphausiids, and because species-specific and size-specific predation rates are largely unknown.

CONCLUSIONS

Among the several characteristics of the ichthyoplankton investigated at contrasting habitat sites, only one, larval production rate, was clearly different between sites. Growth and

mortality rates were statistically indistinguishable between sites. Mortality due to starvation was about the same at the two sites. Larval production at Site 1 was well above the CalCOFI survey average, but Site 2 production and larval mortality at both sites were similar to those over the entire CalCOFI region.

Habitat characteristics at the two sites differed substantially. Site 1 was relatively eutrophic, as seen by its high concentrations of larval forage, zooplankton, chlorophyll, and phaeopigment. Site 2 was much more energetic, as seen by its greater wind speed, current speed, mixed layer depth, and depth of maximum stability. With the exception of predatory copepod abundance, every measured characteristic of the environment favored larval anchovy well-being more at Site 1 than at Site 2.

Yet the well-being of anchovy larvae was about the same at the two sites. Anchovies spawned under conditions where their larvae could grow and survive at about the same rates, despite the differences noted in the respective environments. Similar larval growth rates and the low incidence of starving larvae indicate adequate forage availability in both habitats. In agreement with MacCall's (1983) Basin Model, rates of larval anchovy mortality at the two sites were not greatly different and the same fraction of the original larval production survived to the schooling stage.

We consider this work to be a pilot effort to stimulate and guide research that we hope will be more experimental in scope and execution. To test our hypotheses, environments that more completely span the "suitable basin" need to be described and occupied long enough to follow characteristics of larval fish cohorts from egg to metamorphosis.

ACKNOWLEDGMENTS

This work is dedicated to the memory of Dr. Reuben Lasker: he was our friend and guide. We acknowledge and appreciate the willing hands and shipboard skills of Ken Bliss, Bill Flerx, Dennis Gruber, Sherri Hamer, Sue Longenotti, Jack Metoyer, Patty Schmitt, and the most excellent crew of RV *David Starr Jordan*. We thank Jim DuFour of Scripps Institution of Oceanography for providing the drifters, radio tracking equipment, and tutorials. We thank Rich Charter, Paul Fiedler, Larry Eber, Sherri Hamer, Carol Kimbrell, Lee Inness-Brown, and Pedro Paloma for technical support ashore. The paper also benefited from the comments of our anonymous reviewers.

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Abalone (Genus *Haliotis*) Mariculture on the North American Pacific Coast

David L. Leighton

ABSTRACT: First commercial attempts to culture native Pacific coast abalones were undertaken in California in the mid-1960s. These pioneering groups established basic techniques and stimulated the development of a half-dozen abalone production operations, still chiefly in California. Refinements to the culture technology have resulted from research and development by the industry, but also through studies conducted by nonprofit research groups and government and university programs. This paper briefly examines recent trends in world abalone fisheries and the requirement for mariculture, then describes and evaluates the principal elements contributing to the technological advancement of abalone mariculture in North America.

Substantial advances have been made in the artificial propagation of members of the genus *Haliotis* during the past two decades in the United States, Japan, Australia, New Zealand, and France. Faced with the necessity to supplement the fishery catch or to avert anticipated declines in supplies of this valuable marine resource, efforts in several countries are being directed toward development of effective hatchery programs for production of juvenile stock for use directly in fishery enhancement (through seeding) or for grow-out and production by mariculture. Profit incentives alone have spurred the evolution of private sector intensive abalone culture in the United States.

By far the greatest national effort to increase abalone production has occurred in Japan. Over 30 fisheries laboratories and "Fisheries Farming Centers" throughout that country are concentrating efforts on generation of juvenile abalone (seed) for release in the sea (Uki 1981; McCormick and Hahn 1983). Collectively, these facilities produce about 30 million seed annually (Uki 1981; Grant 1981). Authoritative reviews are also provided by Ino (1980) and Saito (1984).

The Pacific abalone, *Haliotis discus hannai*, is the primary species cultured in Japan, China, and Korea (Sheehy and Vik 1981). Recent attempts to culture the pauas (chiefly *H. iris*) in New Zealand (Anon. 1986) as well as *H. ruber and H. laevigata* in Tasmania (D. Cropp 1987[1]) are showing encouraging results. The ormer, *H. tuberculata*, is being produced in initial programs in Britain and France (Flassch and Aveline 1984). Other experimental and incipient commercial attempts to culture native and introduced species are in progress in Canada (Fletcher 1987), Mexico (Aguirre 1988), and Chile (Owen et al. 1984).

On the Pacific coast of the United States several species of abalones have been subjects of experimental and commercial aquaculture for almost two decades, chiefly the red, *H. rufescens*, and the green, *H. fulgens*. The red abalone is the largest member of the genus and, historically, the major fishery species. First attempts to cultivate abalone in the Western Hemisphere involved this species (Owen et al. 1971; Leighton 1977, 1987). The green abalone, native to temperate waters of southern California and northern Mexico, is broadly tolerant of temperature (Leighton 1974). Some new commercial enterprises are focusing on green abalone production to capitalize on its versatility, relatively rapid growth, and ready marketability. Until quite recently, only in the United States have abalone been cultured to adult size (5–10 cm) by intensive methods for direct marketing as seafood products. Operations elsewhere in the world have focused on producing seed for restocking programs, but it is anticipated that newly established operations for full grow-out will soon expand in Japan, Australia, New Zealand, and Canada.

STATUS OF THE FISHERY

Abalones, all in the genus *Haliotis*, are herbivorous marine gastropods which have long

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[1]D. Cropp, Shellfish Aquaculture Investigations, Tasmania Department of Fisheries, 23 Old Wharf, Hobart 7000, Tasmania.

been utilized as food by man. Nearly 90 species and subspecies are recorded as living in the world today. Paleontological records indicate the presence of the genus since the Cretaceous (Cox 1962). Most extant species live in shallow waters, feeding on marine algae common on rocky substrates from the intertidal to depths over 50 m.

A staple item in the diet of coastal native American tribes, abalone have also been of major importance as food, medicine, and elements of ritual in Asia for centuries. In modern times, extensive exploitation in many countries has resulted in a marked reduction of fishery stocks. Prior to the onset of abalone population decline in California, annual harvests generally exceeded 4.5 million pounds (>2,000 t, see below). In Japan, annual yields have been over 10 million pounds, supplemented now by an intensive nationwide habitat improvement and seeding program (Uki 1981). Production, chiefly from fisheries, has exceeded 44 million pounds (20,000 t) annually (FAO 1975). Worldwide, the market for abalone and abalone products is estimated at more than $300 million (NMFS 1982[2]). Countries most productive in this fishery have been Japan, Mexico, Australia, South Africa, and the United States.

[2]National Marine Fisheries Service. 1982. Southwest Regional Headquarters, Long Beach, CA. (Unpubl. rep.)

In North America, fisheries continue to provide the major supply of abalone, although aquaculture is gaining rapidly as a significant new source, currently estimated at about 5% of the total harvest. Commercial quantities of abalones have been found chiefly along the coasts of California and northern Baja California, Mexico. A small fishery exists in Canada for the pinto abalone, *H. k. kamtschatkana*, (Mottet 1978).

Large-scale exploitation of abalones in California has been in progress for almost a century. Intertidal and shallow subtidal populations were severely depleted by Asian harvesters around the turn of the century. As diving techniques improved and the number of divers increased, especially following World War II, deep-water populations were similarly impacted (Cicin-Sain et al. 1977). An alarming decline was seen in the early 1970s, and annual harvests dropped to less than one million pounds after 1974 (Fig. 1). Comparable declines have been experienced in Mexico, Japan, and elsewhere in the world were intensive fisheries for abalones have developed. However, the demand for abalone remains strong, especially in Asian countries. Japan now imports quantities almost equal to the domestic harvest (Uki 1981).

Circumstances surrounding the decline of the California abalone populations have been unique. Red abalone, once abundant off the central California coast, supported the bulk of the commer-

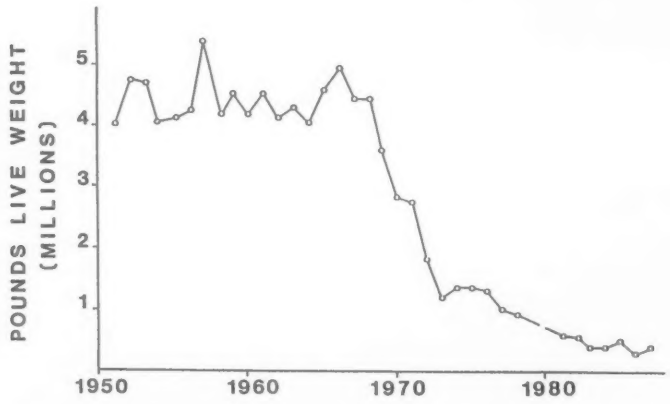

FIGURE 1.—California commercial landings for red, green, and pink abalones, 1951–87. Red abalone predominated in catch until 1975. During 1981–87 average annual landings of red abalone dropped to 329,410 pounds (in-shell) while black abalone take averaged 414,620 pounds. Data from Cicin-Sain et al. (1977) and California Department of Fish and Game, Marine Statistics, Commercial Fish Landings, 1982–87. Other records for 1976–81 from Fish Bulletin 168 and 170, and unpublished logs. Reports for 1979 and 1980 not available.

cial take until about 1965. Thereafter both the toll of increased fishing pressure and increased depredation by the rapidly expanding California sea otter populations significantly reduced red abalone stocks (Cicin-Sain et al. 1977). A combination of pollution, habitat loss, competition with uncontrolled sea urchin population growth, mortalities of undersize abalone due to "bar cuts", and increased harvests by both sport and commercial divers have had a severe impact on stocks of all species of abalones, especially in Southern California (Cicin-Sain et al. 1977). An important additional element in the decline of California abalone populations has been the establishment of seasonal closures which do not adequately protect a large portion of the breeding populations. The midwinter closure for both commercial and sport abalone harvests (mid-January to mid-March) existed for several decades. Since pink (*H. corrugata*), green, and black (*H. cracherodii*) abalones spawn from late spring to late fall (Leighton 1974; Tutschulte 1975), no reproductive protection was afforded by that measure. Only the deep-water, late-winter to spring spawning white abalone, *H. sorenseni*, and a fraction of the year-round spawning red abalone populations, were benefitted by the California abalone "closed season". Currently, a split closure to include one summer month is enforced for the commercial industry, and also for northern California sport divers. The effect of these measures has yet to be assessed. Minimum size limits exist for each species which conserve only the reproductive contribution by young and smaller adults.

THE DEVELOPMENT OF ABALONE MARICULTURE IN CALIFORNIA

It is a commonly held misconception that abalone culture in the United States was modeled after methods established in Japan. However, little technical information on critical aspects of larval and postlarval culture of abalone by Japanese biologists was available to the first entrants into the field in the 1960s. Consequently, the methods developed for culture of all stages of American abalones are quite different from those practiced in Japan (Leighton 1987). More recently, several attempts have been made in California to apply traditional Japanese hatchery methods, but generally the results of these approaches have not been encouraging (see Hatchery Methods, next section).

Pacific Mariculture (Pigeon Point, CA) began to explore possibilities for culture of abalone as seed for reintroduction to native habitat in 1964. Success was achieved in production of juvenile red abalone. Also, spawnings in tanks holding several species yielded hybrid combinations (Owen et al. 1971; Owen and Meyer 1972[3]; Leighton 1987). Experimental planting of juvenile abalone was done, but emigration and mortality at the local offshore site limited returns. At the time, the Department of Fish and Game could not grant exclusive fishery rights to in-sea mariculturists for "undersize native" abalones. Proprietary "nonnatives" (in this case, hybrids) did poorly in the Pigeon Point area. Accordingly, Pacific Mariculture redirected its attention to the production of oyster spat and abandoned further abalone mariculture efforts (B. Owen 1968[4]).

In 1967, California Marine Associates (H. Staton, D. Leighton, and J. Perkins) launched the first large-scale abalone mariculture program in North America with the goal to produce red abalone in land-based tank systems for direct sales to the seafood market. Thousands of seed were provided to the California Department of Fish and Game for their first attempts to plant abalone in the natural environment (Bjornson 1970; Bailey 1973). Commercial quantities of young adult red abalone were soon reared in large concrete raceway tanks. Following an instructive, but problematic, cooperative experimental program with the Atlantic-Richfield Company to conduct containment grow-out of abalone beneath an offshore oil production platform (Gealy and Lindstedt-Siva 1984[5]), California Marine Associates was reorganized to become Estero Bay Mariculture. In 1982, further reorganization occurred and a new company, The Abalone Farm, Inc., was formed. Refinements in the basic culture procedures and expansion of the hatchery and raceway systems have boosted production significantly. In 1986, over 180,000 small adult red abalone (5–10 cm) were marketed, valued at over $400,000 (F. Oakes 1987[6]).

[3]Owen, B., and R. Meyer. 1972. Laboratory hybridization in California abalones (*Haliotis*). Pacific Mariculture, Pigeon Road Point, Pescadero, CA (Unpubl. rep.)

[4]B. Owen, Pacific Mariculture, Pigeon Point Road, Pescadero, CA 94060, pers. commun. 1968.

[5]Gealy, F., and J. Linstedt-Siva. 1984. Containment culture of abalone beneath an offshore platform. Talk presented at Aquaculture Symposium, May 1984, Southern California Academy of Sciences, Los Angeles.

[6]F. Oakes, The Abalone Farm, Inc., P.O. Box 136, Cayucos, CA 93430, pers. commun. 1987.

Ab Lab (J. McMullen, proprietor) began operation in 1972 at Port Hueneme, CA. Initial efforts yielded seed size (2–4 cm) red abalone grown entirely within small tanks. A change to containment culture using mesh-ended polyethylene drums held beneath a dock at the harbor entrance has improved production of larger abalone (4–8 cm). A new market developed in specialty seafood restaurants and sushi bars in the Los Angeles area in the early 1980s. Ab Lab marketed approximately 150,000 young red abalone in 1986 (J. McMullen 1987[7]; Hamilton 1988).

Monterey Abalone Farms began research and development activities for culture of red abalone in 1972. Using an old building on Cannery Row in Pacific Grove, annual production gradually increased, but difficulties stemming in part from what was considered an inordinate volume of governmental restriction and consequent efforts in compliance (Armbrister 1980) prompted a move of the operation to Hawaii. There, an experimental program is underway to apply artificially upwelled seawater to the culture of cold-water mollusks in the tropics (Fassler 1987).

Institutional research efforts related to abalone mariculture have been diffuse. Studies have been based largely at the University of California at San Diego (Leighton 1968, 1972, 1974; Leighton and Lewis 1982) and Santa Barbara (Morse et al. 1977, 1979, 1984), the California Department of Fish and Game laboratory at Carmel (Ebert and Houk, 1984), and World Research, Inc., a San Diego nonprofit research organization (Leighton et al. 1981, Leighton 1985, 1987). Many findings from these studies have added to the fund of knowledge facilitating the development of abalone mariculture.

NORTH AMERICAN SPECIES OF IMPORTANCE TO MARICULTURE

Aside from a single rare and small species occurring in deep water off the Florida Keys (*Haliotis pourtalesii*), North American abalones are to be found only on the Pacific coast. There, seven species and two subspecies of haliotids occur (Fig. 2). In the order of their historical value to California fisheries (prior to 1975) are the red, *H. rufescens*; pink, *H. corrugata*; green, *H. fulgens*; white, *H. sorenseni*; and black, *H. cracherodii*. The remaining species are small and of minor commercial interest.

Descriptions and ranges for the northeastern Pacific abalones are to be found in the literature (McLean 1969; Haaker et al. 1986). An earlier account by Cox (1962) and a later one by Hooker and Morse (1985) contain inaccuracies which make those papers less useful. Generally, the red and black abalones are distributed most broadly, while the green, pink, and white abalones are found only south of the cold-warm transition near Point Conception, CA (Fig. 2.).

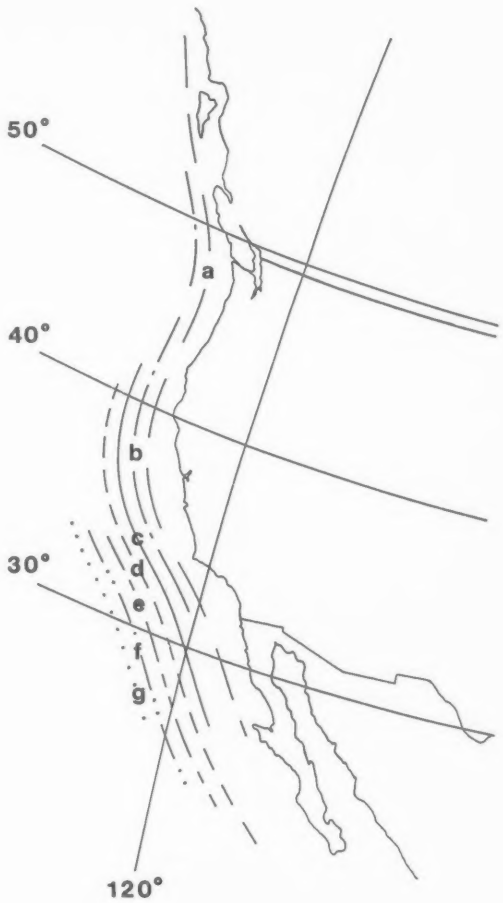

FIGURE 2.—Latitudinal distribution of abalones along the Pacific coast of North America. Range limits are as provided by Haaker et al. (1986). a. *Haliotis kamtschatkana* (two subspecies, *H. k. kamtschatkana* north of Monterey Bay, and *H. k. assimilis* south of that point). b. *H. walallensis*. c. *H. rufescens*. d. *H. cracherodii*. e. *H. fulgens*. f. *H. corrugata*. g. *H. sorenseni*.

[7]J. McMullen, Ab Lab, U.S. Navy Civil Engineering Laboratory, Port Jueneme, CA 93043, pers. commun. 1987.

All California species have now been cultured experimentally, but the red abalone remains as the principal species for mariculture. This cold-water abalone has been the focus of attention chiefly because it thrives along the central California coast where early mariculture operations were most effectively established. Furthermore, most biological information was available for the red abalone and the species was most attractive from the mariculture standpoint, being the largest member of the genus and having the strongest commercial history. It has proved, fortunately, to be the most easily cultured California abalone (Leighton 1987).

The green abalone has shown special potential for mariculture in systems utilizing thermal effluent (Leighton 1974, 1985; Leighton et al. 1981) and other means to provide temperatures in the range 20°–28°C (e.g., thermal enhancement in passive solar or geothermal systems). In the late 1970s, Leighton transported larval and juvenile green abalone to mariculture facilities in Hawaii and Florida, finding survival and growth to be exceptional in those tropical regions (Leighton 1987). The green abalone is especially attractive since its growth rate is significantly increased at higher water temperatures; young adults gain nearly 5 cm/yr in shell diameter (Leighton 1974, 1985; Leighton et al. 1981).

Pink and white abalones have been cultured on a small scale (Leighton 1972, 1974). The black abalone, a shallow-water species of lower commercial grade, is broadly tolerant of temperature in adult stages, but larvae from California races have thermal limits similar to that of the cold-water red abalone. Black abalone have been reared from laboratory-spawned eggs (Leighton 1974, unpubl. data). Flat, *H. walallensis*, and threaded, *H. kamtschatkana assimilis*, abalones have also been cultured in research projects in Southern California. The pinto abalone, *H. k. kamtschatkana*, is receiving attention as a mariculture subject in Washington and British Columbia (Fletcher 1987). All species of eastern North Pacific abalones have been found to hybridize in the laboratory with varying degrees of success. In most cases larvae and subsequent stages are fully viable and young adults fertile (Owen and Meyer 1972 [fn. 3]; Leighton and Lewis 1982). Some hybrids exhibit features which promise to be advantageous to mariculture, including environmental adaptability, improved growth rate and hardiness, and possibly refinements in quality of flesh (Leighton 1987).

AMERICAN ABALONE CULTURE TECHNOLOGY

As stated earlier, methods to culture abalone in California were developed quite independently from those practiced in Japan. Generally, the emphasis by U.S. culturists has been on production of crop animals of small adult size directly marketable in the domestic trade. Abalone are reared to sizes of 7–10 cm either within specialized tanks on shore or in containments held in protected ocean waters. In Japan, however, young abalone are usually released to the natural environment at a size of 2–5 cm for continued growth over periods of 2–4 years until a marketable size (7–10 cm) is reached (Saito 1984). Few attempts have been made in that country to rear abalone to adults under the controlled environmental conditions afforded by appropriate tank systems. However, highly elaborate concrete and plastic structures of many designs to provide protective substrate and improved foraging are now being applied to abalone grow-out in the sea (Sheehy and Vik 1981). Coupled with habitat improvement (i.e., algal afforestation and predator control), these in-sea approaches to increase abalone production are gaining success (see Alternatives for Grow-Out). The economic and other risks associated with such measures have constrained development by private enterprise in the United States.

Hatchery Methods

The requirement of North American species of abalones for rapidly moving, well-aerated seawater led to the early development of culture tanks which provided full circulation. Circular tanks proved most effective, and Leighton (1977) introduced such a tank in which rotary flow was easily maintained by air-lift with minimum energy input. Self-cleaning features accompany the vortical drive, airlift return design (Fig. 3). Originally devised for culture of relatively sessile marine invertebrates, the tank allows maximum control, a rapid circulation, and foam fractionation via the return line. These features are effective for culture of swimming larvae and early settled stages. Following use by us (California Marine Associates), new entrants adopted similar tank designs for postlarval and juvenile culture. Now typical of U.S. hatchery tank arrays, round tanks stand in marked contrast to the "raceways" and immersed plastic panels employed in Japan and elsewhere.

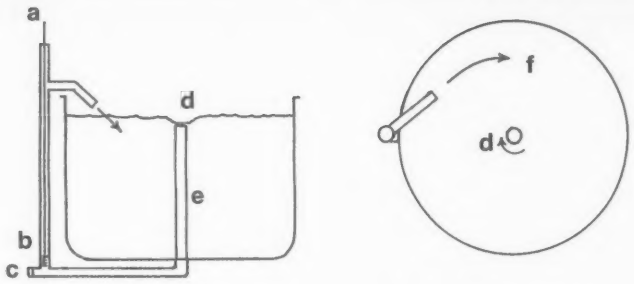

FIGURE 3.—Cylindrical larval and postlarval rearing tank. Vortical drive airlift circulated tank in its simplest form. Tank is self-cleaning and vertical extension for air-lift pipe allows foam fractionation (from Leighton 1965 (unpubl. data), 1977). a. Airline; b. air stone at base of airlift column; c. drain port, normally closed; d. vortex; e. central stand pipe, removable; f. return flow.

Gravid adult abalone may be induced to spawn using several different methods. Thermal shock, still used in some hatcheries in Japan (Ino 1980), was initially used in U.S. abalone culture, but soon abandoned in favor of the method of Kikuchi and Uki (1974) using UV-irradiated seawater. Also available is the hydrogen peroxide method developed by Morse and associates (Morse et al. 1977, 1978). Each approach has its advantages and disadvantages (Ebert and Houk 1984; Leighton and Lewis 1982). Usually broodstock are spawned in separate containers, then gametes are collected and combined to yield the highest fertilization rates. Eggs are subsequently washed and incubated under static conditions at temperatures most appropriate for the species (Leighton 1972, 1974).

Embryos generally hatch from eggs in 12–18 hours as trochophore larvae. Soon after hatching, larvae display a negative geotaxis (Leighton 1972, 1974), swimming at the surface in culture containers for 6–12 hours. This behavior, common to red, green, pink, and white abalones, has been mistakenly regarded as a positive phototaxis in observations with *H. rufescens* by some workers (c.f., Ebert and Houk 1984; Hooker and Morse 1985). Light, however, has a negligible influence on the swimming behavior of these species in the trochophore and pre-eyespot veliger larval stages. Larvae then become increasingly demersal with age. Culture routines, involving water changes and concentration of larvae, take advantage of these behavioral characteristics.

In the hatchery, larvae are generally reared through swimming stages (approximately one week) in culture containers of small volume (5–10 L) with careful attention to water quality, bacterial contaminants, temperature, and density. Highly filtered (ca. 1 μm) seawater, antibiotic treatment, and daily water changes promote maximum survival (virtually 100%) and normal development when larvae are incubated at densities of 2 individuals/mL or less (Leighton 1977). Some laboratories utilize mesh-bottom plastic cylinders immersed in a highly controlled, circulating system similar to that employed in bivalve culture (Ebert and Houk 1984).

The temperature dependency of early development for the principal California species is described by Leighton (1972, 1974). Cold-water species (red, pinto, flat, and white) have thermal optima for larval development in the range of 12°–16°C. The black abalone, while broadly tolerant of temperature in adult stages, is similar to the cold-water species in larval life (optimum 14°–18°C; Leighton 1987). The green abalone is distinctive, having a thermal optimum for larval development in the range of 18°–24°C (Leighton 1974, 1985; Leighton et al. 1981). The pink abalone is intermediate in its thermal requirements. In contradiction to a recent report by Hooker and Morse (1985), only the green abalone among California species may be considered "thermophilic". Hatcheries involved in culture of red, pink, and green abalones must observe the temperature requirements of these species closely.

Advanced larvae are induced to settle and begin metamorphosis using a variety of methods (see Problem Areas). Commonly, larvae at an age of about six days are admitted to small volume tanks supporting thin coatings of benthic microflora (chiefly diatoms and associated bacteria) wherein larvae settle within several hours

to two days. It was observed early in red abalone hatchery research that larvae introduced to tanks precolonized by crustose coralline red algae settled promptly. Tanks which had recently held healthy conspecific juveniles, the walls of which presented a well-grazed microfloral substrate, proved especially beneficial to successful settlement and metamorphosis (Leighton 1987). Several sources of "inducers" which effectively prompt settlement and metamorphosis appear to exist (see Problem Areas).

Settled larvae immediately begin feeding on bacteria and other microflora. Metamorphosis commences with loss of the velar cilia and larval operculum. Deposition of peristomial shell is evident within another day, but metamorphosis is a complex and gradual transition. The first respiratory pore is formed at the end of postlarval life (onset of the early juvenile stage), generally as the abalone reaches 1.5–2.5 mm (age about six weeks).

Postlarval attrition continues to remain as the principal "efficiency bottleneck" in abalone culture. Under usual hatchery conditions, survival and normal development for swimming larvae are close to 100% (Leighton 1977, 1985), but mortalities occur in a large percentage of metamorphosing postlarvae with the result that early juveniles represent at best 5–10% of the number of larvae at settling. Declines are most evident during the fourth to sixth week postfertilization. However, when conditions are optimized (usually in small volume containers), survival through postlarval life may be over 25% (c.f., Leighton et al. 1981; Table 1). Losses during critical early benthic stages may thus be reduced significantly by appropriate control and care to include frequent water changes, maintenance of clean conditions, and supplying microalgal foods on a regular basis (see Problem Areas).

Juvenile Culture

Once postlarval abalone begin to form the first respiratory pore, the pallial system (gills and associated structures) and other features of anatomy become more typical of the adult. The juvenile stage commences at this point and extends to young adulthood and onset of sexual maturity. Dietary changes occur in conjunction with development; first-settled metamorphosing postlarvae feed upon smaller microflora (diatoms, sessile flagellates, and bacteria). Early juveniles rely on many larger microalgae, but undergo a dietary transition to include a variety of green, red, and brown macroalgae as advanced juvenile stages are approached. The dietary transition to macroalgae occurs in many species at about 1 cm shell length (4–6 months), but is usually never complete as microalgal films may be ingested and metabolized through adult life (Leighton 1987).

When juvenile abalone reach about 3 mm, they are transferred to larger tanks precolonized by appropriate algae. Transfer is achieved with negligible losses by simple brushing (Leighton

TABLE 1.—Size increase for young adult red and green abalones provided two brown algal diets.

		Mean shell length gain (μm/d)					
		Haliotis rufescens period			*Haliotis fulgens* period		
Alga	Group	I	II	III	I	II	III
Macrocystis pyrifera	A	64.9	57.7	61.7	33.4	45.9	54.0
	B	35.8	71.0	65.9	31.4	17.8	36.8
$\bar{x}$	(S.D.)		59.5	(12.4)		36.6	(12.5)
Egregia menzesii	A	76.3	91.9	81.5	86.4	101.6	93.0
	B	60.5	97.3	78.8	71.4	90.0	66.0
$\bar{x}$	(S.D.)		81.1	(12.9)		84.7	(13.5)

Mean shell length increases (μm/d) for young adult abalone held in duplicate groups (6 individuals/group). Abalone were fed to satiation throughout three feeding periods of 40–50 days each. All abalone were in the size range 5–10 cm; groups were held in 10 L plastic pails receiving ambient seawater at 1 L/min and vigorous aeration. To promote continuous feeding, freshly collected algae were provided in excess (ca. 100 g) weekly. *Haliotis rufescens* observations were made in winter, 13°–17°C; *H. fulgens* in summer and fall, 18°–22°C.

1977, 1985). Some culturists employ chemical relaxants (such as Benzocaine at 100 ppm) to facilitate transfer, but associated losses may be high. The latter method becomes necessary when original culture tanks are large and immovable.

Japanese methods for abalone culture, outlined by several researchers (Kan-no 1975; Ino 1980; Grant 1981; Uki 1981), almost universally employ elongate rectangular "raceway" tanks holding vertically suspended corrugated plastic panels for culture of postlarvae and juveniles. Larvae are allowed to settle directly on the plastic substrates in special tanks prior to transfer to the raceways. Young abalone are reared to 1–2 cm under those conditions. While some hatcheries release the juveniles in the sea for fishery enhancement at that point, others retain the abalone in mesh-bottom drums held upright in larger tanks or supported by rafts in protected marine areas for growth to 3–5 cm (Kan-no 1975).

In the two principal hatcheries for red abalone in California (The Abalone Farm and Ab Lab), culture through early juvenile stages is achieved employing similar systems. However, these groups differ markedly in their approaches for rearing young abalone to market size (4–10 cm). The Abalone Farm practices raceway culture in which juveniles are reared in a series of concrete troughs through which seawater cascades from upper to lower members. Vigorous aeration is supplied intermittently and seawater flow rates vary from 0 to 200 L/min, depending on the pumping schedule. The kelp, *Macrocystis pyrifera*, is the principal food provided, although many species of red, green, and brown algae are available locally in large quantity and are supplied supplementally. Ab Lab transfers juvenile red abalone at about 1 cm to containment structures held in the channel at the entrance to Port Hueneme Harbor. Large polyethylene drums (ca. 55 gal capacity) with plastic or stainless steel mesh capped ends are secured in a horizontal position to braces in racks, all immersed to a depth of a few feet beneath a pier. Each drum receives several thousand individuals initially. *Macrocystis* forms the majority of the diet. Thinned with growth, the young abalone are reared to a size of 4–5 cm and sold live to specialty seafood dealers in the Los Angeles area (Hamilton 1988).

The relatively slow growth rate typical of abalones (ca. 2.5 cm/yr) has been limiting to commercial production by mariculture. However, some species exhibit accelerated development and growth at water temperatures higher than normally experienced in nature. The Pacific abalone has been reared in thermal effluent seawater from an electric power plant in Japan during the cold season (McBeth 1972). Growth rate of the California green abalone was almost doubled when reared at 24°–28°C in power plant effluent in an extensive 4-yr study (Leighton et al. 1981; Leighton 1985). Two new programs in abalone mariculture are being established to utilize thermal energy from coastal power facilities in Southern California for commercial production of this valuable species (see Future Prospects).

ALTERNATIVES FOR GROW-OUT

High costs of grow-out in most land-based systems make methods to rear abalone from juveniles to marketable adult stages in the sea attractive. As discussed earlier, emphasis in Japan has been placed on the design and testing of a diversity of artificial habitats for environmental improvement and partial containment for abalone in the ocean. In that country the largely government-supported hatcheries supply seed abalone to members of fishery cooperatives for planting on improved and controlled areas of sea bottom (Saito 1984; Sheehy and Vik 1981). The introduced abalone are allowed to mature for a period of 2–4 years before final harvest. Much attention has been given means for enhancing survival and growth of these crops by increasing production of kelps and other seaweeds as well as expanding the substrate necessary for concentrated "farming" of abalone. Yields of marketable abalone have been increased appreciably in some areas as these two approaches are coupled with measures to harvest or otherwise reduce numbers of predatory fish and invertebrates (Ino 1980; Uki 1981).

In the mid-1960s, significant advances were made in the United States toward kelp habitat improvement (North 1976). Areas of rocky bottom maintained in minimal algal productivity by large concentrations of sea urchins are often those with the highest potential for algal production and abalone recruitment. A valuable tool for restoration of ecological balance resulted from the finding by Leighton that calcium oxide effectively reduced numbers of overgrazing echinoids, fostering the return of *Macrocystis* and other vegetation with subsequent repopulation by diverse fauna (Leighton et al. 1966; Leighton 1971). Red and pink abalone populations returned to the Point Loma Shelf (San Diego) with

unusually heavy recruitment following treatment in 1963–65 of the area with quicklime to reduce sea urchin numbers (Leighton 1968). Interest is gaining in Japan to reclaim vast areas of potentially productive sea bottom limited by sea urchins (e.g., the "isoyake", or "pink rock", coralline algae/echinoid-dominated bottom) for increased abalone production using several approaches of physical habitat improvement, chemical treatment, and algal afforestation (Uki 1986[8]).

Several groups holding leases to areas of offshore California land are engaging in "sea-floor ranching" of abalone. In 1984, a total of about 50 acres had been leased for this purpose in southern California (Leighton 1984[9]). One individual (D. Gilbert, San Diego Mariculture) has liberated many millions of late-stage larvae onto rock bottom within boundaries of his lease holdings. Increases in population densities of seeded species are reported in preliminary surveys. Larval seedings often fail for a number of reasons, including "temporary settlement" (clinging while retaining the ability to swim once again; Leighton 1987), micropredation, and variable viability of different larval stocks. A successful field plant of larval *H. iris* in New Zealand has been reported (Tong et al. 1987). In that experiment, localized recruitment occurred, likely because larvae were released at an advanced age (13 days, Tong 1987[10]), thus reducing the opportunity for emigration.

It appears success of larval and juvenile plantings is dependent on a variety of factors (see Problem Areas). Extremely high losses of red abalone juveniles were reported soon after release off the California coast by Department of Fish and Game biologists (Tegner and Butler 1985). Introduction of young abalone to the marine environment is, however, quite unlike releasing trout fry in freshwater lakes and streams. Using "temporary protective habitats", Leighton (1985, 1987) found greatly improved survival of green abalone through reduced handling during transport and minimized predation during the critical 1–2 days following plants. This highly effective and low cost method uses shelters consisting of stacked corrugated PVC sheet (Fig. 4) which allow high density containment during transport and initial protection at the planting site, virtually eliminating "planting mortality". Survival one year after release, based on live recoveries, has been at least 20%; a highly conservative estimate since the planting areas were sampled without destructive approaches to open crevices or upturn large rocks (Leighton 1985, 1987). Likely a combination of controlled planting, habitat improvement, algal afforestation, and predator reduction will prove most effective for the success of seafloor ranching of abalone in California.

Experimental U.S. programs in containment culture carried out by private interests have included buoyed cages (Pacific Ocean Farms, Monterey), cylindrical modular habitats (Atlantic-Richfield Company/California Marine Associates, Santa Barbara), and bottom-secured concrete pipe sections. Containment culture in the sea presents advantages for concentration and protection not inherent in the more extensive approach of seafloor ranching. Under appropriate routines for feeding and maintenance, abalone may be reared at high densities, greatly simplifying the harvesting process. However, containment culture has, to date, proven expensive, not entirely free of predation problems (as young stages of crabs, seastars, etc. enter cages), and subject to destruction by heavy surge and entanglement by drifting kelp. Groups conducting studies in California have not solved all these problems. New designs of containment structures, which incorporate effective feeding systems, are simply monitored and are less susceptable to damage by physical forces are needed to advance technology in this area.

PROBLEM AREAS

The major technological impediments to full development of efficient abalone mariculture in North America appear to fall into three categories: 1) Yields of juveniles under hatchery conditions generally represent less than 10% of the larval stock; 2) conditions for optimization of the culture environment to promote maximum health and growth still require definition for each of the principal species cultivated; and 3) cost-effective methods and associated materials for grow-out, especially in the ocean, remain to be tested and applied on a commercial scale.

Abalone culture technology advanced rapidly

[8]N. Uki, National Research Institute of Aquaculture, Nansei, Mie 516-01, Japan, pers. commun. 1986.

[9]Leighton, D. L. 1984. Recent developments advancing aquaculture of abalone in southern California. Paper presented to Marine Aquaculture–Southern California, 1984 Symposium. Annual Meeting, Southern California Academy of Sciences, May 12, 1984, Los Angeles.

[10]L. Tong, Ministry of Aquaculture and Fisheries, Fisheries Research Center, P.O. Box 297, Wellington, New Zealand, pers. common. 1987.

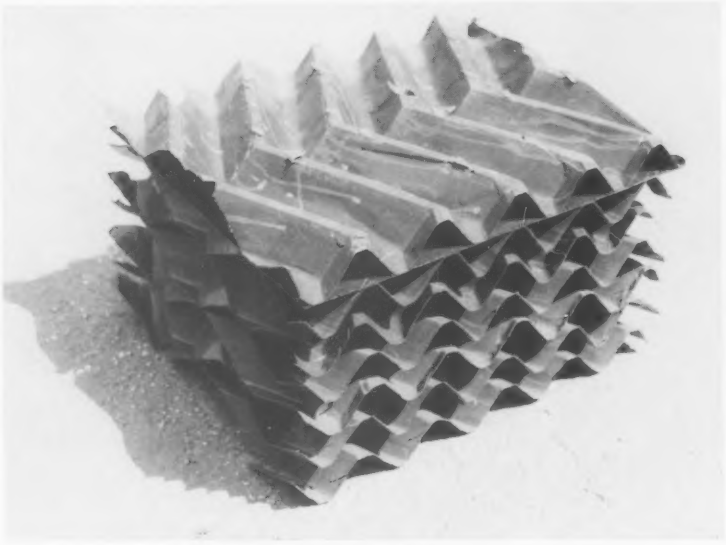

FIGURE 4.—Corrugated PVC sheet "temporary shelter" used to corral juvenile abalone in the hatchery, act as containment structure in transport, and serve as a stocking module and protective habitat for abalone planted in the marine environment. Over 200 juveniles (1–2 cm) may be contained in a single unit 20 × 20 × 30 cm. Abalone planted in these modules move to surrounding natural habitat within 24–48 hours without the high handling and predation mortality experienced with other methods (Leighton 1985). The layered plastic material is manufactured by B. F. Goodrich Company as "Bio-trickling Filter Medium" for use as a high surface to volume bacterial substrate applicable to sewage treatment processes. [Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.]

in the private sector in the period 1970–75; highly effective methods were found to allow rearing of young red and green abalones through larval and early postlarval stages (ca. days 1–15) with minimal losses (Leighton 1987). These procedures have understandably been closely guarded by the pioneering U.S. abalone culturists. Recently, reports have appeared of new and grand technological advances in abalone culture through research in government (e.g., Ebert and Houk 1984) and academic laboratories (e.g., Hooker and Morse 1985). However, with the exception of the highly useful hydrogen peroxide method for induction of spawning in abalones (see Hatchery Methods), these studies have not, to date, added significantly to the technology for culture of larvae, postlarvae, and juveniles developed by the industry. Certainly, however, the research has contributed valuably to our understanding of basic biological processes (see below).

Interest has focused recently on the facilitation of settlement and prompting of metamorphosis by the addition of bioactive chemicals such as the neurotransmitter, gamma-aminobutyric acid (GABA) and related compounds (Morse et al. 1979). GABA does indeed cause a change in swimming behavior, possibly by affecting the bioelectric potential of cell membranes associated with the velar cilia (Koshtoyants 1960; Baloun and Morse 1984), with active settlement in mature and "competent" larval abalone. Behavior of larvae exposed to GABA, however, differs from that of larvae in the presence of "natural" inducers (see below). Exposure of larvae to GABA at concentrations in excess of 10^{-5} M is in fact lethal (Akashige et al. 1981; Slattery 1987), perhaps a consequence of excessive activation and/or blocking of receptor and transduction sites involving other vital functions. The role of GABA as a neurotransmitter is now well recognized in vertebrate and invertebrate systems. However, induction of settling and onset of metamorphosis in abalone larvae may be more complex than initially proposed (see Trapido-Rosenthal and Morse

1986) and may involve yet unidentified mediators and environmental cues. Further insight regarding use of GABA and other bioactive substances to prompt settlement and metamorphosis may be gained from the analysis and discussion by Pawlik (1988).

The behavior of larvae at settlement is critical to subsequent survival. In the presence of many elements common to the native environment of abalone, including microfloral colonies (diatoms, bacterial films, etc.), biliprotein-containing crustose red algae and cyanobacteria (Morse et al. 1984) and even "mucous trails" of conspecific juveniles (Seki and Kan-no 1981; Leighton 1985; Slattery 1987), advanced larvae of *H. rufescens* and other species examined exhibit a typical swimming behavior consisting of a series of landings and takeoffs as if testing the substrate prior to settlement. Surface acceptance is independent of orientation; settlement may be on container sides, bottom, or even on the undersides of included substrates. In contrast, in the presence of GABA, larvae often settle promptly (usually within 2 hours at 10^{-6} M), but almost exclusively on container bottoms. In the hatchery setting, the tank bottom rapidly becomes a hostile environment and larvae settled there soon succumb to bacterial overgrowth. Using diatom films and other natural substrates, dispersal is optimized and subsequent settling and metamorphosis are normal (Leighton 1977, 1985). GABA is not used routinely in commercial facilities for the reasons cited above.

In California abalone hatcheries, larvae at competence are admitted to tanks appropriately prepared for settling and metamorphosis containing partially cleared diatom coatings (Leighton 1977), other microflora, or traces of mucus and associated substances left by former conspecific occupants (Leighton 1985, 1987; Slattery 1987). In the early stages of red abalone mariculture (Leighton, pers. obs. 1970–75) crustose coralline red algae (*Lithothamnion* and related forms) were cultured within special postlarval culture tanks. Settlement on coralline surfaces was often intense, and subsequent survival and growth of postlarvae was excellent. However, juveniles larger than 5 mm derived decreased nutriment from the coralline-benthic diatom substrate, necessitating their transfer to tanks precolonized by diverse microflora and to which macroalgae were supplied as foods. This observation is in confirmation of results (Leighton 1968: table XXX) showing reduced nutritional benefit of crustose coralline algal substrates for juvenile *H. rufescens*. It was also found in early hatchery operations that larval settling and postlarval success were greatly improved in fiberglass tanks which had recently held conspecific juveniles and adults (Leighton, pers. obs. 1971). More recently, Japanese biologists have found a similar benefit for larval recruitment to exist in *H. discus hannai* (Seki and Kan-no 1981).

As noted earlier, postlarval attrition still limits the efficiency of abalone mariculture, although claims to the contrary appear in the literature (e.g., Hooker and Morse 1985). Losses of 60–80% of postlarvae are commonly experienced during the second to sixth weeks following fertilization (Leighton 1985). While microbial pathogens have not often been demonstrated, a portion of the postlarval attrition may be due to disease. Mortalities may be reduced by providing intensive care to small-scale cultures for which antibiotic prophylaxis or other procedures are followed to minimize epizootic complications. A parasitic protozoan found especially lethal to juveniles younger than 190 days, but not injurious to more mature abalone, was isolated from an abalone hatchery in British Columbia (Bower 1987). Since many potentially deleterious organisms (e.g., *Vibrio* spp.) appear to thrive in decomposing organic matter, the well-managed hatchery is not likely to experience epidemic outbreaks of bacterial and protozoan diseases.

Regardless of the approach, a major portion of the postmetamorphic young eventually succumb before passing early juvenile stages (Leighton 1985). In practice, the high fecundity typical of mature female abalone acts in compensation for the large losses, and spawnings of small numbers of broodstock supply commonly several million larvae on each occasion.

The U.S. species of abalones most produced by mariculture, the red and the green, differ markedly in their requirements of nutrition as well as temperature (Leighton 1987). Kelps commonly used as foods for abalone in California mariculture are *Macrocystis pyrifera* and *Egregia menzesii*. The former is a valuable food for young red abalone, but a relatively poor diet for green abalone (Table 1). *Egregia* is effectively utilized by both species and is the diet of choice for culture of green abalone (Leighton et al. 1981). *Laminaria farlowii*, common in southern California, is also a productive diet, especially for green abalone. Mixed algal diets yield superior growth (Leighton 1968, 1977).

In hatchery systems, holding abalone at high stocking densities and providing satiation feeding, optimization of flow and exchange rates, pH, oxygenation, and other factors is essential for best animal health and growth. Often all requirements appear not to be met in tank rearing systems, however. Growth rate and vitality are generally greatly improved when abalone are matured in the sea in appropriate containments (see Alternatives for Grow-Out).

Growth of the industry in Southern California has been limited by land availability, water quality, and regulatory constraints. Central and northern California offer a far greater extent and variety of coastal sites, but temperature optimization, food availability, salinity reduction, and, at some locations, pollution add to operational limitations. Aside from certain locations within Puget Sound, WA and contiguous areas of Canada, most coastal regions in the Pacific Northwest present similar problems. Failure of some recent mariculture ventures has been due, in part, to inattention to some of these considerations.

FUTURE PROSPECTS

Successes in production and marketing by the existing abalone mariculture concerns in California are stimulating interest among new groups. At least three additional groups are planning shore-based abalone culture operations in the state at this time: Pacific Mariculture, Inc., Santa Cruz (P. Scrivani 1988[11]); Abalone Resources, Inc., Guadalupe; and Marine Bioculture, Inc., Carlsbad. Most will concentrate on production of small adult red abalone. Marine Bioculture will produce green, pink, and red abalones. Total annual production from expanded activities at the Abalone Farm, the Ab Lab, and the newer organizations could reach 100 t by 1995 and 250 t by the year 2000. Harvests from seafloor ranching of red abalone may increase rapidly and match the onshore production by that time. Thenceforth, yields from expanded in-sea programs (both containment culture and seafloor ranching) are expected to gain appreciably as the pertinent technology and cost/benefit factors are improved, and as seed stock becomes more universally available from the land-based hatcheries.

[11]P. Scrivani, Pacific Mariculture, Inc., 100 Shaffer Rd., Santa Cruz, CA 95060. PMI is distinct from PM, Pigeon Point, CA.

The potential for effective abalone mariculture both onshore and in the sea off Baja California, Mexico, is exceptional. To date mariculture of red, pink, green, and black abalones has been largely experimental in that country, but it is expected commercial operations will develop there soon (Aguirre 1987).

A forecast of significant growth in the abalone production industry over the next decade applies to the entire North American Pacific coast from Baja California to Alaska. The frontier now lies in the sea with a promising evolution of effective approaches to both managed cultivation by seafloor ranching and concentrated production within containing structures.

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A Key to Genera of the Penaeid Larvae and Early Postlarvae of the Indo-west Pacific Region, with Descriptions of the Larval Development of *Atypopenaeus formosus* Dall and *Metapenaeopsis palmensis* Haswell (Decapoda: Penaeoidea: Penaeidae) Reared in the Laboratory

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ABSTRACT: The penaeid prawns *Atypopenaeus formosus* Dall and *Metapenaeopsis palmensis* Haswell were induced to spawn and their larvae and postlarvae were cultured in the laboratory. Three protozoea, three mysis, and early postlarval substages are described for each species. A key to genera of the penaeid larvae and early postlarvae of the Indo-west Pacific region was constructed from this information, from other unpublished data from our own larval reference collection, and from previously published larval descriptions. The key, based entirely on laboratory-reared larvae, identifies the genera *Atypopenaeus, Macropetasma, Metapenaeopsis, Metapenaeus, Parapenaeopsis, Parapenaeus, Penaeus,* and *Trachypenaeus*. A sternal spine formula, a previously undescribed taxonomic character, is used for identifying postlarvae.

Twelve genera of penaeid prawns are found in the Indo-west Pacific: *Atypopenaeus*, *Funchalia*, *Heteropenaeus*, *Macropetasma*, *Metapenaeopsis*, *Metapenaeus*, *Parapenaeopsis*, *Parapenaeus*, *Penaeopsis*, *Penaeus*, *Trachypenaeopsis*, and *Trachypenaeus*. Most of these genera are widespread and common; the exceptions are the monospecific genus *Macropetasma*, which occurs only near the southern coast of South Africa, and *Heteropenaeus* and *Trachypenaeopsis*, which are widespread but rare (Dall el al. in press).

In spite of the worldwide distribution, abundance, and commercial importance of penaeids, ecological studies of their larvae have been hampered by taxonomic problems (Rothlisberg et al. 1983a). Several keys to larval penaeid genera have been published; however, none of these are suitable for use in the Indo-west Pacific region. Cook's (1966a) key to the Gulf of Mexico penaeid genera was a milestone, and remains the most useful reference. However, many Indo-west Pacific genera do not occur in both regions (e.g., *Atypopenaeus* and *Metapenaeus*) and therefore could not be included. *Xiphopenaeus* is included but does not occur in the Indo-west Pacific. *Sicyonia* and *Solenocera*, which Cook included, are now regarded as separate families in the superfamily Penaeoidea (Bowman and Abele 1982).

The keys of Hassan (1974), Haq and Hassan (1975), and Muthu et al. (1978) dealt with three genera in the Indo-west Pacific—*Penaeus*, *Metapenaeus*, and *Parapenaeopsis*—while Paulinose (1982) covered all genera except *Heteropenaeus* and *Macropetasma*. He also included the nonpenaeids *Sicyonia*, *Aristaeomorpha*, and *Solenocera*. However, many of the identifications in Paulinose's work are based on doubtful reconstructions from the plankton and the key has several practical shortcomings (see Discussion).

Penaeus and *Metapenaeus* have worldwide commercial importance in fisheries and aquaculture, and the larvae of many species have been reared in the laboratory and described (for review see Dall et al. in press). There have been very few laboratory studies that describe the larval morphology of the remaining penaeid genera in the Indo-west Pacific region. *Parapenaeopsis stylifera* larvae were reared and described by Rao (1973) and Hassan (1984). Thomas et al. (1975) also reared the larvae in the laboratory but provided no figures or detailed descriptions. *Macropetasma africanum* was reared and described by Cockcroft (1985). Heldt (1938) described *Parapenaeus longirostris*, but all

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stages after protozoea I are based on exuviae of a single surviving specimen. *Trachypenaeus* larvae were described by Kirkegaard (1969), but only the protozoea I were reared in the laboratory; later stages were isolated from preserved plankton catches. The only other description of *Trachypenaeus* is by Pearson (1939), who also used a combination of plankton-caught and laboratory-reared larvae. The present study is the first description of larvae of any species of either *Atypopenaeus* or *Metapenaeopsis*, based on laboratory-reared specimens.

To date, our published studies of larval prawns in the Gulf of Carpentaria have dealt exclusively with the genus *Penaeus* (Rothlisberg et al. 1983a, 1985, 1987; Rothlisberg and Jackson 1987). The characteristics of this genus are well established and their larvae are quite distinct from those of other genera (Cook 1966a). In order to study other genera, we have reared larvae of all six penaeid genera which are found in the Gulf of Carpentaria: *Metapenaeus*, *Metapenaeopsis*, *Penaeus*, *Atypopenaeus*, *Trachypenaeus*, and *Parapenaeopsis*. For all but one genus we now have a reference collection of protozoea I through to postlarvae; for *Parapenaeopsis* we have only the nauplius and protozoeal stages (Rothlisberg et al. 1985).

In assembling this key to genera of Indo-west Pacific penaeid larvae, we have used both our own reference material and information from previously published descriptions and keys. We have relied completely on existing descriptions for *Macropetasma* (Cockcroft 1985) and *Parapenaeus* (Heldt 1938; Pearson 1939; Paulinose 1979), genera not represented in the Gulf of Carpentaria and hence absent from our reference collection. Several workers who have described larvae from plankton samples claim to be able to identify the genus or even the species of the larvae. In the absence of supporting evidence from laboratory-reared larvae we have not used these descriptions in constructing our key. No reliable information about *Funchalia*, *Heteropenaeus*, *Penaeopsis*, and *Trachypenaeopsis* is available as they have never been reared in the laboratory.

MATERIALS AND METHODS

Gravid female *Metapenaeopsis palmensis* selected from trawl catches near Groote Eylandt in the western Gulf of Carpentaria in November 1983 and from off Cairns, northeast Queensland, in April 1985 were brought to the Cleveland laboratory. Gravid female *Atypopenaeus formosus* were collected from commercial trawl grounds in Moreton Bay, adjacent to the Cleveland laboratory, in January 1985.

When female prawns arrived at the laboratory, one eyestalk was ablated and the prawns were placed in a 90 L fiberglass aquarium with 4 cm of clean sand substrate. Seawater in the aquarium was continually replaced at approximately 1 L per minute, and any eggs or larvae were retained by a 90 μm mesh screen on the overflow. Prawns were fed daily on a frozen mixture of prawn and squid. The aquarium water was inspected each morning for eggs. When eggs were detected they were examined microscopically and, if embryonic development was normal, the female prawns were removed and preserved. When the eggs hatched, the nauplii were siphoned off, their abundance was estimated, and they were transferred into culture vessels at a density of approximately 100 nauplii per liter.

The culture vessels used were round-bottomed, 100 mm diameter Pyrex[1] tubes of 3 L capacity, with aeration supplied through a nipple molded into the bottom of the tube. The tubes were placed in environmental cabinets that enabled control of temperature (27°C) and of photoperiod (12 h:12 h light:dark). On alternate days, approximately 2.5 L of water were drawn off from the larval cultures through a 140 μm screen, and replaced with 1 μm filtered seawater.

For larval food, the marine alga *Tetraselmis suecica* was produced by batch culture in 20 L glass carboys. During the log growth phase, 13 L of algal culture were removed and the algal cells concentrated using a modified cream separator. The aerated concentrate was stored at 4°C and used as stock for feeding the larvae. The stock was replaced every 3–4 days.

Twice daily, beginning at late nauplius stage and continuing through to postlarva, sufficient algal concentrate was added to the larval cultures to maintain an algal cell density of approximately 1.5×10^5 cells per mL. Cell density in the larval cultures was estimated by fluorometry based on the relationship between fluorescence and cell density (P. C. Rothlisberg[2]). After the larvae reached mysis I, freshly hatched, heat-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[2]Rothlisberg, P.C., Division of Fisheries, CSIRO Marine Laboratories P.O. Box 120, Cleveland, QLD 4163, Australia, unpubl. data.

killed *Artemia* nauplii were added daily, to a final concentration of 2–5 nauplii per mL.

Larval samples were removed from the cultures twice daily and preserved in 2% formaldehyde. At this sampling frequency, at least two samples were taken from any substage. For microscopic examination the preserved larvae were cleared in a polyvinyl alcohol solution to which Chlorazol Black had been added (Perkins 1956), and permanent slides both of whole animals and of dissections were made in this medium. For each larval substage described, at least five individuals were examined except where fewer larvae in good condition were available (Tables 1, 2). Where possible, the larvae examined came from different spawnings; otherwise, they came from the same spawning but were taken at different times.

Figures were drawn with the aid of a camera lucida used on a Wild M20 compound microscope. Measurements were made with a calibrated ocular micrometer. Body length was measured from the anterior border of the carapace (excluding the rostrum) to the posterior border of the telson, excluding any spines, and carapace length was measured to the posterior border of the carapace, along the midline.

RESULTS

General development

Atypopenaeus formosus and *Metapenaeopsis palmensis* followed the normal development pattern for penaeid larvae (Dall et al. in press): a number of nauplius substages, three protozoea substages, three mysis substages, and a series of postlarva substages gradually leading toward the juvenile form. While it may be possible to identify unknown penaeid nauplii into groups of one or more genera, preliminary studies confirmed the findings of Cook (1966a) that reliable generic identification of nauplii is not possible. To increase the numbers of cultured larvae available for sampling in later substages, the nauplius substages were not sampled and therefore are not described.

The protozoea I of both species was characterized by separate cephalothorax and abdomen, undeveloped eyes (which may be visible beneath the carapace), and a lack of uropods. Protozoea II had stalked eyes and a rostrum, while protozoea III had spines on a variable number of the abdominal segments and separate uropods. Mysis I lacked abdominal pleopods, mysis II had pleopods of a single segment, while the abdominal pleopods in mysis III had two segments. During the postlarval substages the pleopods became setose and the pereopod exopods became reduced. We have not attempted to describe specific instars or molt numbers of the postlarvae. Instead we have presented a single description which is representative of the first few instars; it is based on larvae sampled within two to three days of the first appearance of postlarvae. Earlier or later instars will, of course, differ in some respects. The most obvious changes with age are that the length of the 2nd antennal flagellum increases, the dorsal rostral spines increase in number, the telson becomes more pointed, the number of telson spines decreases, and the number of telson setae may increase.

Atypopenaeus formosus

The details of setation and segmentation for the various appendages are given in Figures 1 to 7 and in Table 1. Only general features, and those with some taxonomic significance, are described in the text below. For each major stage, the important features that do not vary between substages are presented first, followed by a brief description of the characteristics of each substage.

PROTOZOEA. Second antenna 0.7–1.0 times length of 1st in each substage. Setal formula of 2nd antennal protopod and endopod 1+2+2 [hereafter referred to as the 2nd antennal formula: the numbers of setae at the distal end of the protopod (Fig. $1d_1$), partway along the 1st endopod segment (Fig. $1d_2$), and at the distal end of the 1st endopod segment]. Second antennal exopod (Fig. $1d_3$) with 9 or 10 setae along inner margin, including those on distal segment. Telson with 7+7 setae in each protozoeal substage.

Protozoea I (Table 1, Fig. 1a) with pear-shaped carapace, less than half of total length, bearing a pair of frontal organs without overlying spines. Long labral spine present (Fig. 1b). Mandible asymmetry not yet pronounced, each mandible having a single, freestanding tooth between incisor and molar processes (Fig. 1e). First maxilla (Fig. 1f) protopod with 2 lobes, epipod (Fig. $1f_1$) with 4 long setae; 2nd maxilla protopod with 5 lobes (Fig. 1g). Segmentation of 1st and 2nd maxillipeds indistinct and variable (most common arrangement

TABLE 1.—Summary of larval characteristics of *Atypopenaeus formosus*. BL = body length (mm), number to left of colon indicates number of segments and numbers to right are setal counts for each served on different individuals. "*" indicates more than 10 setae too densely clustered to count appendage. Setal numbers are totals of all setal types on any segment. Reference to figures will

	Protozoea I (Fig. 1)	Protozoea II (Fig. 2)	Protozoea III (Fig. 3)	Mysis I (Fig. 4)
Number examined	8	8	10	8
BL mean (range)	0.7 (0.6–0.9)	0.9 (0.8–1.2)	1.6 (1.4–1.7)	2.0 (1.8–2.1)
CL mean (range)	0.3 (0.2–0.4)	0.4 (0.4–0.5)	0.6 (0.5–0.6)	0.6 (0.6–0.8)
First antenna				
Proximal part	3:1,2,5	3:1,6,5	4:0–2,1–3,3,5	3:6–7,4,3–5
Outer ramus	—	—	—	1:3
Inner ramus	—	—	—	1:1
Second antenna				
Protopod	2:0,1	2:0,1	2:0,1	2:0,0
Blade (seg: inner,outer)	9:9–10,2	9:9–10,2	10–12:9–10,2	1:8–11,1
Flagellum	2:4,4	2:4,4–5	2:4,4–5	1:4
Mandible				
Movable teeth (a:b)[1]	1:1	1:5	2:6	3:7
Palp	—	—	—	—
First maxilla				
Protopod	1:4–6/4	1:5–6/5–6	1:4–6/7–9	1:5–7/8–10
Endopod	3:2,1,4–5	3:2,1,4–5	3:2,1,5	3:1–2,0–1,4–5
Epipod	1:4	1:4	1:4	1:4
Second maxilla				
Protopod	1:6–7/1–2/3/ 3–5/2	1:8–10/2–3/2–4/ 4–7/2–3	1:9–10/3–4/4/ 4–5/2–3	1:12–14/4–6/5–10/ 7–8/3
Endopod	4:3,2,1–2,3	4:2,1–2,2,3	4:2–3,2,2,3	4:2,1–2,2–3,2–3
Epipod	1:4	1:5	1:5	1:7
First maxilliped				
Protopod	1–2:1–2,5–8	2:4–6,6–9	2:5–8,9–12	2:6–8,10–15
Endopod	4:3,1–2,2,5	5:3,2–3,2–3,2,4–5	4:3,2,1–2,5	4:2,2,1–2,3–4
Exopod	1:7	1:7	1:9	1:10
Second maxilliped				
Protopod	2:1,3	2:0–2,3	2:3,4–7	2:2–3,5–7
Endopod	4:1,1,1,5	4:1–2,1,1–2,5	4:2–3,1,2,4–6	4:4,3,1–2,3–4
Exopod	1:5–6	1:6	1:6–7	1:7
Third maxilliped				
Protopod	—	1:0	1:0	2:0,2–5
Endopod	—	1:0	1:3–4	5:1–2,2,1–2,3,4–5
Exopod	—	1:2–3	1:3–6	1:5–9
First percopod				
Protopod	—	—	—	2:0,0
Endopod	—	—	—	1:5–7
Exopod	—	—	—	1:11–15

[1]"a" side fewer teeth, "b" side more teeth. No attempt was made to match mandibles to either left or right sides.

CL = carapace length (mm). For each entry, unless otherwise indicated, segment from proximal to distal. "–" indicates range of setal numbers ob- reliably. Numbers separated by "/" are setal counts for separate lobes of an show distribution of setae along segments.

	Mysis II (Fig. 5)	Mysis III (Fig. 6)	Postlarva (Fig. 7)
Number examined	6	4	5
BL mean (range)	2.0 (1.8–2.1)	2.3 (2.2–2.4)	2.2 (1.9–2.7)
CL mean (range)	0.6 (0.6–0.7)	0.7 (0.6–0.8)	0.7 (0.6–0.8)
First antenna			
Proximal part	3:10–13,3–6,4–8	3:5–13,3,4–6	3:10–16,5–9,1
Outer ramus	1:4	2:0,4	3:0,0,3–5
Inner ramus	1:2–3	1:0	3:0,2–6,3–4
Second antenna			
Protopod	2:0,0	2:0,0	2:0,0
Blade (seg: inner,outer)	1:10–16,0	1:15–17,0	1:21–25,0
Flagellum	2:0,0–1	3:0,0,0	4:0,3,2,2
Mandible			
Movable teeth (a:b)[1]	2:7	3:6	0–1:1–5
Palp	—	1:0	2:2–5,5–15
First maxilla			
Protopod	1:6–7/8–14	1:6–7/10	1:7/10
Endopod	3:1–2,1–2,3–5	3:2,1,3–4	3:1,2,4
Epipod	0–1:4	—	—
Second maxilla			
Protopod	1:*/*/*/*	1:*/*/*/*	1:*/*/*/*
Endopod	4:2,1–2,2–3,2–3	4:2,1,0–1,3	1:*
Epipod	1:10–15	1:10–15	1:*
First maxilliped			
Protopod	2:6–8,8–12	2:5–8,13–15	1:*/*
Endopod	4:4,1–4,1–4,4	4:3,1–2,1–2,4–5	4:2,2,0,4
Exopod	1:6–7	1:5–7	1:5
Second maxilliped			
Protopod	2:2–3,5–7	2:3,4–5	2:4,*
Endopod	4–5:3,4,0–3, 3,4–5	5–6:3–4,3,0,2–3, 1–3,3–5	5:1,4–6,1,3,5
Exopod	1:3–5	1:4	1:5
Third maxilliped			
Protopod	2:0,2	2:0,1	2:1,3
Endopod	4:2,1,1,6	5:1,1–2,2–3,0,5	5:3,4,4,1,5–7
Exopod	1:3–6	1:4–7	1:6
First percopod			
Protopod	2:0,1	2:0,0	2:3,4
Endopod	2:2,3	4:0,1,2,4–7	4:1,3,5,3
Exopod	1:6–8	1:6–8	1:6

TABLE 2.—Summary of larval setation and segmentation of *Metapenaeopsis palmensis*. BL = body indicated, number to left of colon indicates number of segments and numbers to right are setal counts observed on different individuals. "*" indicates more than 10 setae too densely clustered to count appendage. "t" indicates terminal segment. Setal numbers are totals of all setal types on any seg-

	Protozoea I (Fig. 8)	Protozoea II (Fig. 9)	Protozoea III (Fig. 10)	Mysis I (Fig. 11)
Number examined	10	4	6	8
BL mean (range)	0.8 (0.7–0.8)	1.4 (1.4–1.5)	2.0 (1.9–2.1)	2.3 (2.1–2.7)
CL mean (range)	0.4 (0.3–0.4)	0.5 (0.5–0.6)	0.7 (0.6–0.7)	0.7 (0.6–0.8)
First antenna				
Proximal part	3:0–1,2,5	3:0–1,1–3,4–6	4:1,1,3,4–5	3:10–12,4,4–6
Outer ramus	—	—	—	1:4–5
Inner ramus	—	—	—	1:1–2
Second antenna				
Protopod	2:0,1	2:0,1	2:0,1	2:0,0
Blade (seg: inner,outer)	9:9–11,2	8–9:9–11,2	8–10:9–11,1	1:10–11,1
Flagellum	2:4,5	2:4,5	2:4,5	1:4
Mandible				
Movable teeth (a:b)[1]	1:2	1:4	2:6	3:7
Palp	—	—	—	—
First maxilla				
Protopod	1:5–7/3–5	1:6/6–7	1:4–8/8–10	1:6–8/8–12
Endopod	3:2–3,2–3,4–5	3:2,2,4–5	3:2,1–2,3–5	3:2,1–2,4
Exopod	1:4	1:4	1:4	1:4
Second maxilla				
Protopod	1:5–7/3/3/2–4/2	1:6–8/2/3–4/2/3–5	1:8–10/2–4/3–6/ 3–6/2–4	1:*/3–5/3–5/4–6
Endopod	4:1–2,1–2,2–3,3–4	3:1–2/1–2/2–3	4:2–3,2,2–3,2–3	4:2,1–3,1–3,3–4
Exopod	1:4	1:5	1:5	1:12
First maxilliped				
Protopod	1–2:12–17	2:5–9,8–9	2:5–11,8–10	2:8,11–13
Endopod	4:3–4,1–2,1,5–6	4:3,1–2,1–2,5	4:2–3,1–2,1–2,5	3–4:3,1–3,1,3–4
Exopod	1:7	1:7	1:8–10	1:10–11
Second maxilliped				
Protopod	1–2:5–7	2:4,3	2:3–4,5–7	2:4,7–8
Endopod	4:1–2,1–2,1–2,5	3–4:2,1,1,4–5	4:3,1–2,1–3,4–5	4:4,2,3–4,5
Exopod	1:6	1:6	1:8–9	1:5
Third maxilliped				
Protopod	—	1:0	2:0,0	2:0,4–5
Endopod	—	1:0	1:3	4–5:2,2–3,2–3,2, 4–5
Exopod	—	1:2–3	1:4–5	1:5
First pereopod				
Protopod	—	—	—	2:0,2
Endopod	—	—	—	3:2,2,7
Exopod	—	—	—	1:7

[1]"a" side had fewer teeth, "b" side had more teeth. No attempt was made to match mandibles to either left or right

length (mm), CL = carapace length (mm). For each entry, unless otherwise for each segment from proximal to distal. "–" indicates range of setal numbers reliably. Numbers separated by "/" are setal counts for separate lobes of an ment. Reference to figures will show distribution of setae along segments.

	Mysis II (Fig. 12)	Mysis III (Fig. 13)	Postlarva (Fig. 14)
Number examined	5	4	3
BL mean (range)	2.7 (2.5–2.8)	2.8 (2.7–2.9)	2.8 (2.6–3.0)
CL mean (range)	0.7 (0.7–0.8)	0.8 (0.7–0.8)	0.7 (0.7–0.8)
First antenna			
Proximal part	3:6–10,8–12,4–6	3:12–16,5,5	2:17–25,8–12
Outer ramus	1:4–6	1:5	2:0,4
Inner ramus	1:1–2	1:3	1:2
Second antenna			
Protopod	2:0,0	2:0,0	2:0,0
Blade (seg: inner,outer)	1:15–18,0	1:16–21,0	1:25–28,2
Flagellum	4–5:0,0,0,0,2	5–9:3t	15–25:(all 0–1),6t
Mandible			
Movable teeth (a:b)[1]	3:7	3:7	0–3:0–6
Palp	—	1:0	2:5–9,12–20
First maxilla			
Protopod	1:4–8/8–10	1:6–8/8–11	1:4–8/9–13
Endopod	3:2,2,3	3:2,1–2,3–5	1:0–7
Exopod	—	—	—
Second maxilla			
Protopod	1:*/5/6–8/2–4/1–2	1:*/2–4/5–7/4–5/2	1:3–5/3–5/4–8
Endopod	3:2–4,2–4,3	3–4:(all 1–3)	1:4
Exopod	1:11	1:10	1:25–35
First maxilliped			
Protopod	2:8–9,10–16	2:5–9,13–16	1:20–25/10–15
Endopod	4:3–4,2–3,1,4	3–4:3,2,1,5	3:2,0,1
Exopod	1:7–10	1:8–10	1:5
Second maxilliped			
Protopod	2:3–4,8–10	2:3–5,8–10	2:1,7
Endopod	5:4,2–3,2,1–2,6	5:4,3–5,2–3,2–3,4–6	5:2–4,5,0,3,4–6
Exopod	1:6	1:5	1:0
Third maxilliped			
Protopod	2:0,2–3	2:0,1–2	2:1,0
Endopod	5:1–2,1–2,1–4,3,5	5:1–2,2–3,2–3,2,4	6:(all 3–6), 6t
Exopod	1:4	1:4–6	1:0
First pereopod			
Protopod	2:0,2	2:0,1–2	2:2,3
Endopod	4:1,1–2,2,3–4	4:0–1,1–2,2–3,4	4:2,0,2,6
Exopod	1:4	1:7–8	1:0

sides.

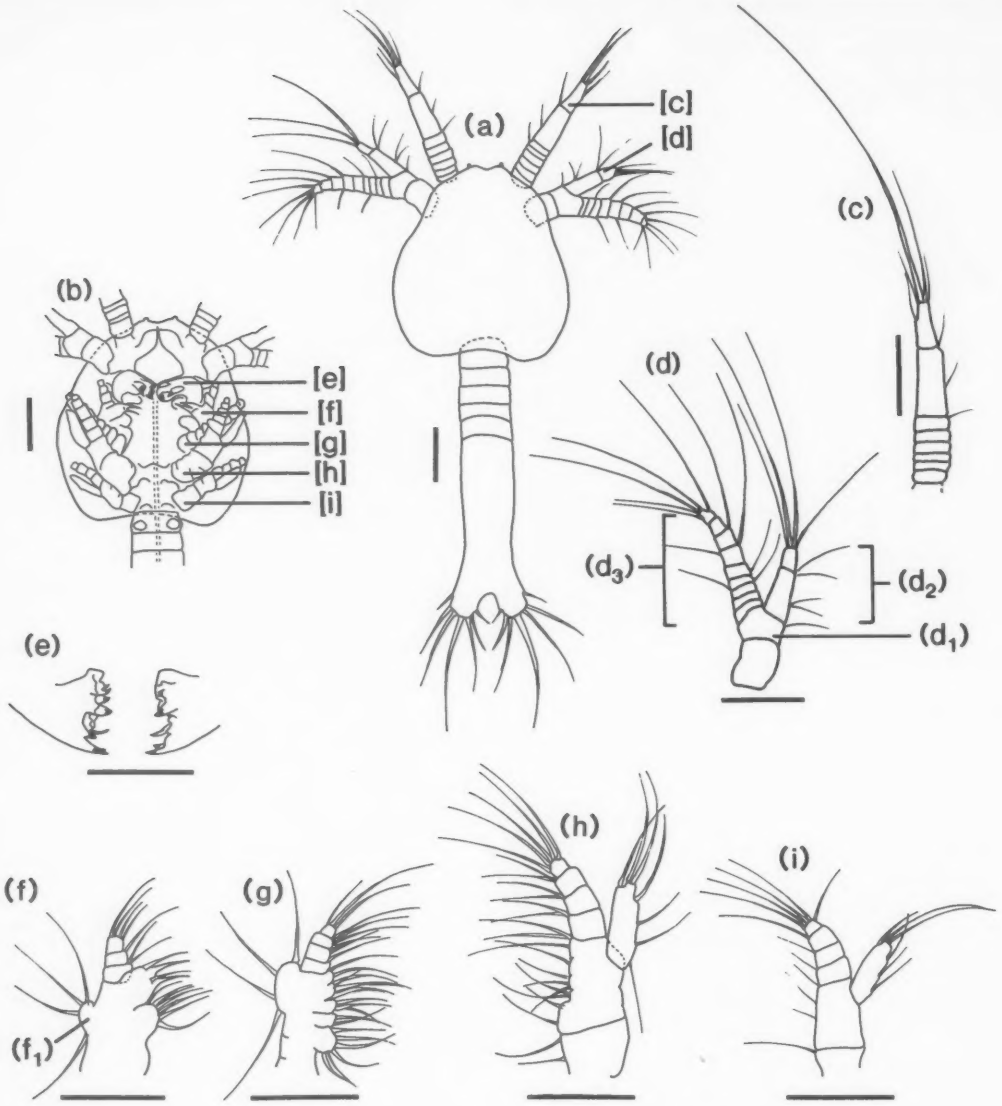

FIGURE 1.—*Atypopenaeus formosus* protozoea I. (a) whole animal, (b) ventral view of cephalothorax, (c) 1st antenna, (d) 2nd antenna, (d_1) protopod, (d_2) endopod, (d_3) exopod, (e) mandibles, (f) 1st maxilla, (f_1) epipod, (g) 2nd maxilla, (h) 1st maxilliped, (i) 2nd maxilliped. Letters in square brackets show origins of dissected appendages. Scale = 0.1 mm.

shown: Fig. 1h, i). Third maxilliped only a bud (Fig. 1b).

Protozoea II (Table 1, Fig. 2a) with long rostrum, extending beyond eye, and a single pair of supraorbital spines. Second antennal formula still 1+2+2 but first seta very small, sometimes difficult to see (Fig. 2c). Mandibles (Fig. 2d) now asymmetrical, one side with 5 serrate, free-standing teeth, other side only 1 (no attempt was made in any dissection to determine whether a particular mandible was originally from the left or the right side). First and 2nd maxillae (Fig. 2e, f), 1st and 2nd maxillipeds (Fig. 2g, h) similar to previous substage. Third maxilliped slightly more developed, biramous, however, still very small (Fig. 2i).

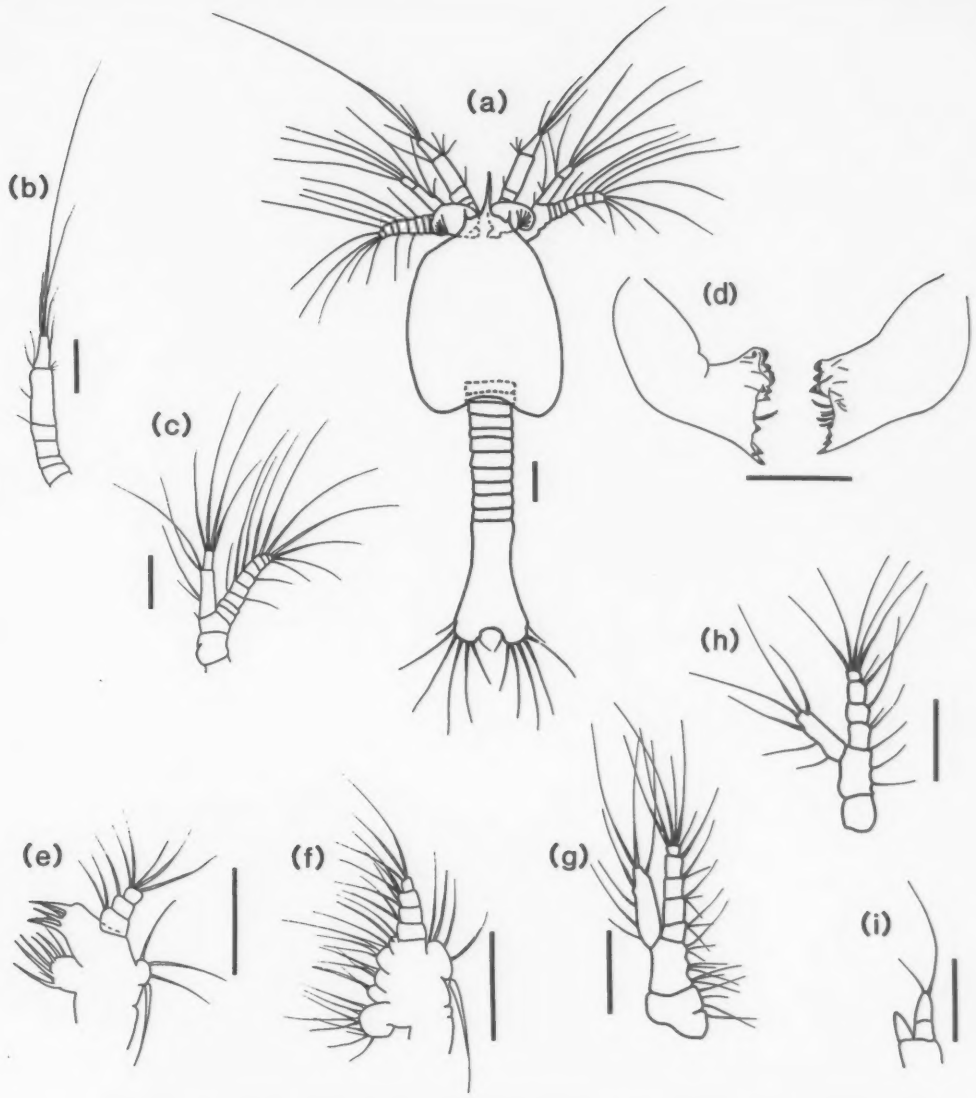

FIGURE 2.—*Atypopenaeus formosus* protozoea II. (a) whole animal, (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped. Scale = 0.1 mm.

Protozoea III (Table 1, Fig. 3a) retaining long rostrum and supraorbital spines. Some setae in 2nd antennal formula of 1+2+2 are small but always present (Fig. 3c). Maxillae (Fig. 3e, f), maxillipeds (Fig. 3g, h, i) similar to previous substage, although generally more robust and more setose. Dorsal spines occasionally on 4th abdominal segment and always on 5th; lateral spines on 5th and 6th segments (Fig. 3a). Uropods present (Fig. 3a).

MYSIS. Characteristics that are invariant in the mysis stage of *A. formosus* are rostrum extending beyond eye, lack of supraorbital and hepatic spines, presence of pterygostomial spine, 7+7 telson spines, 6th abdominal segment always

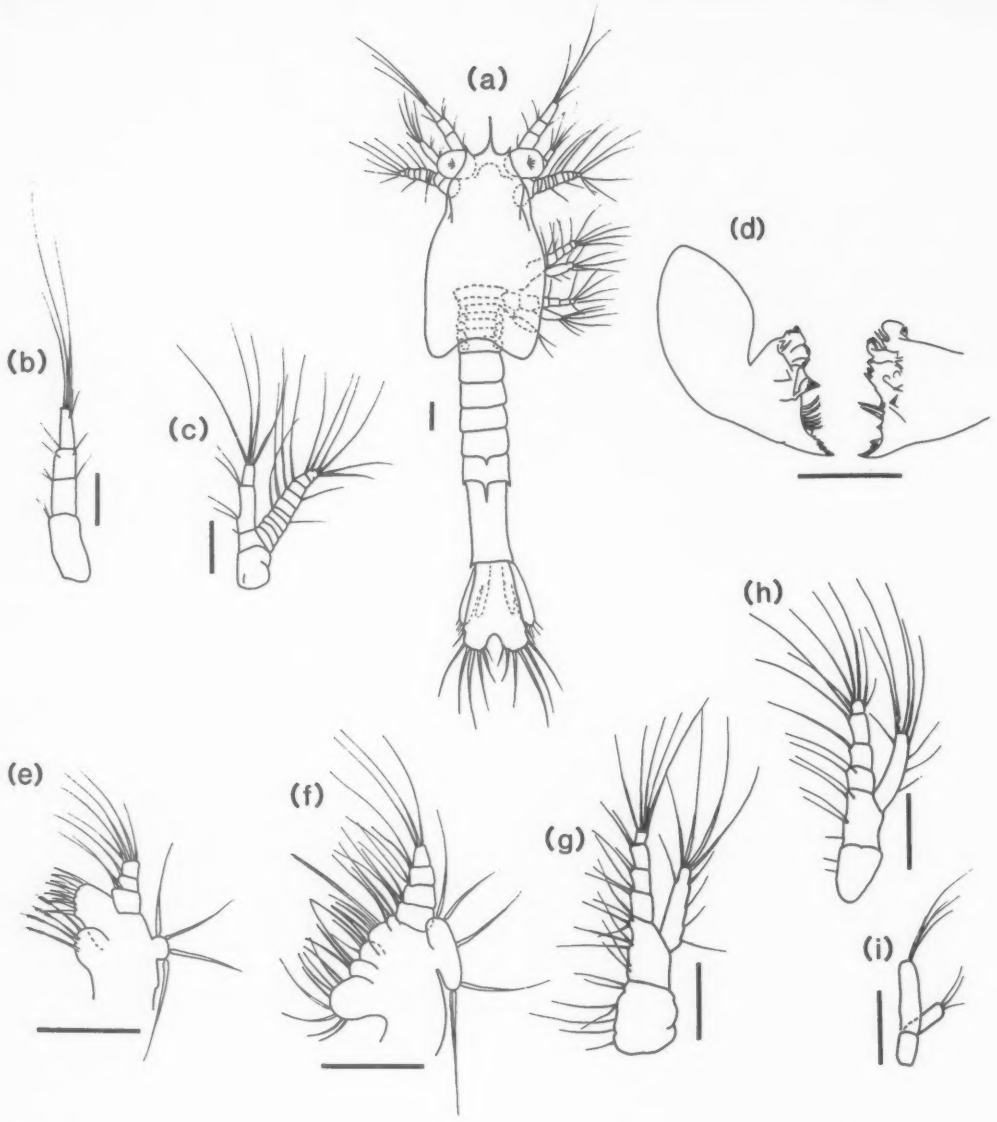

FIGURE 3.—*Atypopenaeus formosus* protozoea III. (a) whole animal, (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped. Scale = 0.1 mm.

bearing a dorsal spine, lack of lateral abdominal spines.

Mysis I (Table 1, Fig. 4) without rostral teeth. First antenna biramous, bearing a strong ventral spine on first segment (Fig. 4c). Second antenna devoid of segmentation on both endopod and exopod (Fig. 4d). Mandibles similar to those of protozoea III, although stronger and with more teeth (Fig. 4e). Structure of 1st maxilla (Fig. 4f) similar, but epipod on 2nd maxilla, the formative scaphognathite, is beginning to increase in size (Fig. 4g). First 2 maxillipeds similar to previous substage but 3rd much more elongate (Fig. 4h, i, j). Rudiments of chelae appearing on 1st 3 pereopods (Fig. 4k). Usually a small dorsal spine on 5th abdominal segment,

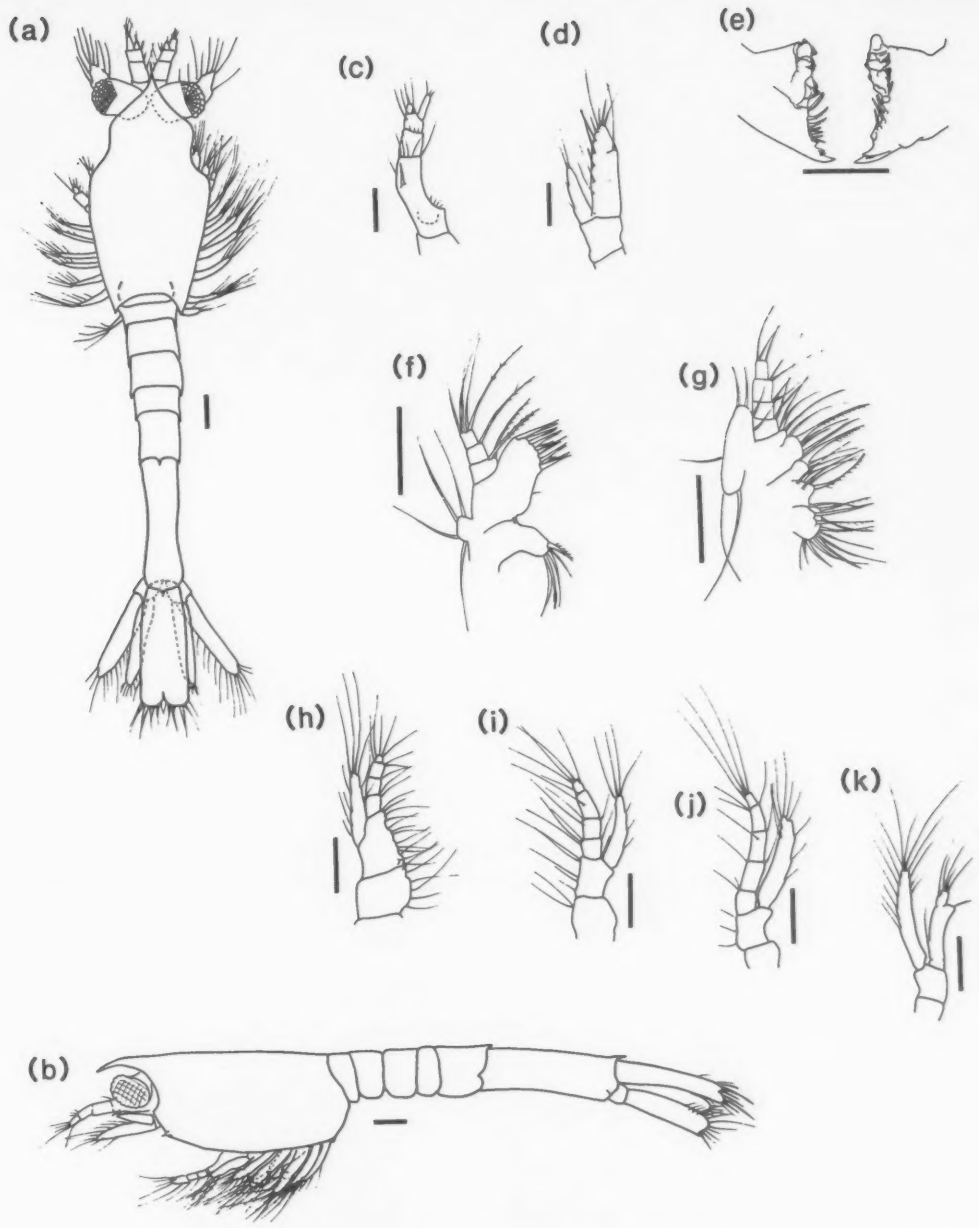

FIGURE 4.—*Atypopenaeus formosus* mysis I. (a) whole animal (dorsal view), (b) whole animal (lateral view), (c) 1st antenna, (d) 2nd antenna, (e) mandibles, (f) 1st maxilla, (g) 2nd maxilla, (h) 1st maxilliped, (i) 2nd maxilliped, (j) 3rd maxilliped, (k) 1st pereopod. Scale = 0.1 mm

and a large one on the 6th. Telson retaining deep cleft with 7+7 spines (Fig. 4a).

Mysis II (Fig. 5) still with no rostral teeth. Dorsal spine on 5th abdominal segment either missing or very small; spine on 6th segment remains. Small statocyst sometimes present in 1st antenna (Fig. 5b). Second antenna with spine on blade, flagellum of 2 segments about half as long as blade (Fig. 5c). First maxilla now without epipod, although a small protuberance sometimes remains (Fig. 5e). Epipod of 2nd maxilla further enlarged, more setose (Fig. 5f). First maxilliped stouter than previous, exopod much reduced in size (Fig. 5g). Second and 3rd maxillipeds changing little (Fig. 5h, i); chelae on pereopods clearly defined (Fig. 5j).

Mysis III (Fig. 6) with 2 dorsal rostral teeth. Only 6th abdominal segment with dorsal spine.

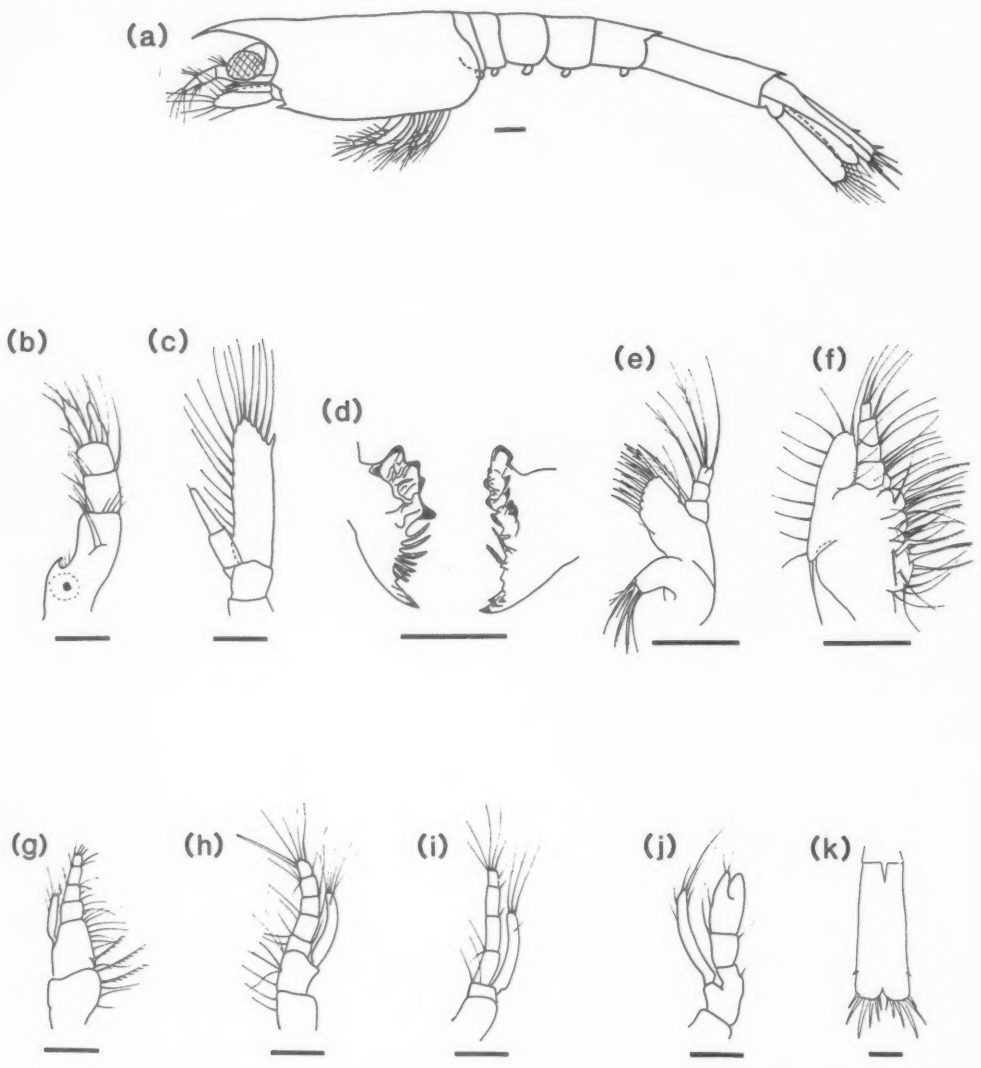

FIGURE 5.—*Atypopenaeus formosus* mysis II. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

Statocyst now normally present (Fig. 6b), antennal flagellum about the same length as in previous substage (Fig. 6c). Mandible with unsegmented palp (Fig. 6d). First maxilla similar to previous substage (Fig. 6e); epipod of 2nd maxilla continues to become larger and more setose (Fig. 6f). Three maxillipeds now bearing rudimentary gills (Fig. 6g, h, i), which vary in size in different individuals; pereopods now have functional chelae (Fig. 6j). Shallow telson cleft remains (Fig. 6k).

POSTLARVA. The postlarva of *A. formosus* (Fig. 7) has a rostrum with 3 dorsal teeth and an epigastric tooth. Pterygostomial spine present, but no supraorbital or hepatic spine. Proximal

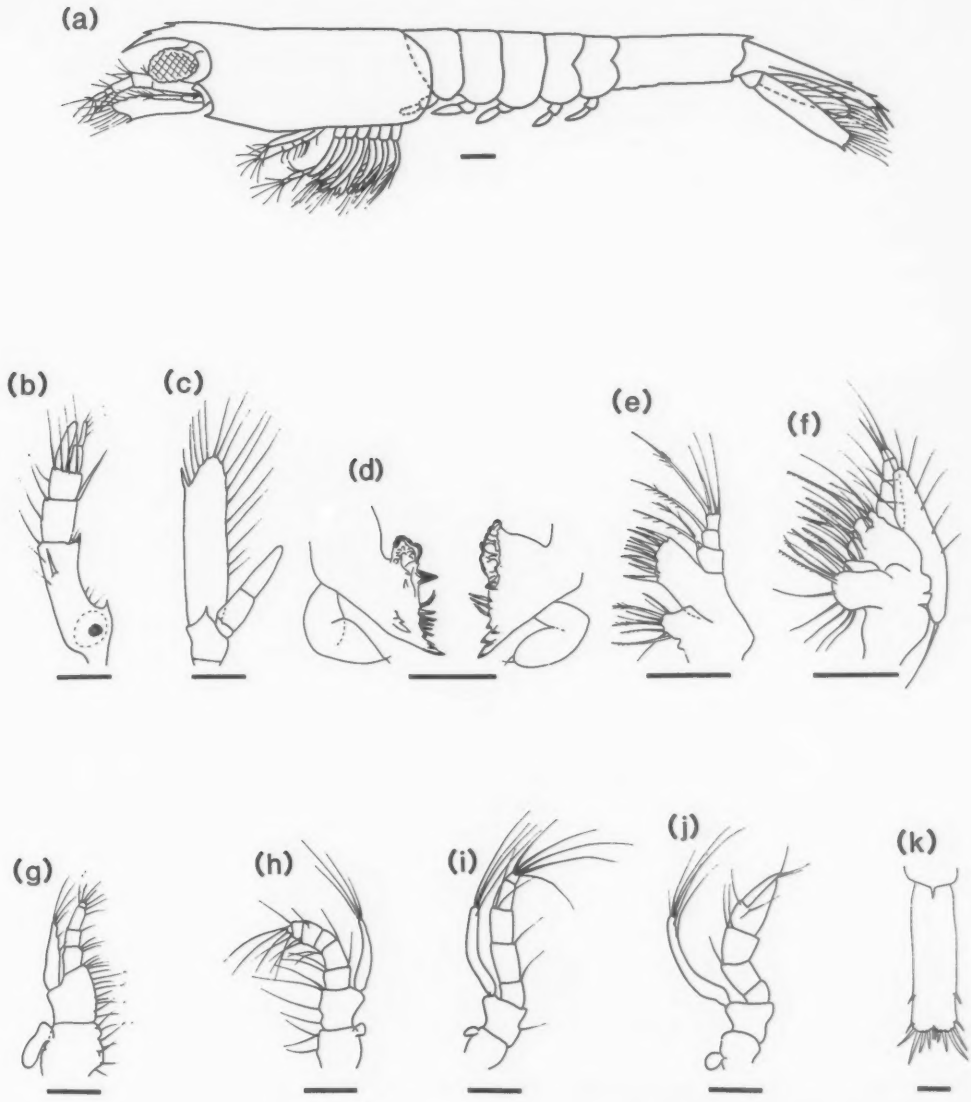

FIGURE 6.—*Atypopenaeus formosus* mysis III. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

segment of 1st antenna with 1 spine near statocyst, 1 distally; 2 rami now elongated (Fig. 7b). Antennal flagellum almost as long as blade (Fig. 7c). Most fine teeth and grinding teeth absent from mandible, now bearing 2-segmented, setose palp (Fig. 7d). First maxilla (Fig. 7e) unchanged; epipod of 2nd maxilla (Fig. 7f) extends from base to tip. Exopod and endopod of 1st maxilliped reduced in size (Fig. 7g). Second maxilliped little changed (Fig. 7h), endopod of 3rd maxilliped long and slender (Fig. 7i). Pereopods and chelae longer and stronger (Fig. 7j). One long median sternal spine on 4th thoracic segment, and 1 short median sternal spine on 5th (sternal spine formula 0+0+0+1+1) (see Figure 15e). Only 6th abdominal segment with dorsal spine (Fig. 7a). Posterior margin of telson rounded, without cleft. Telson spine formula remaining 7+7 with additional 2 long, feathery submedian setae (Fig. 7k).

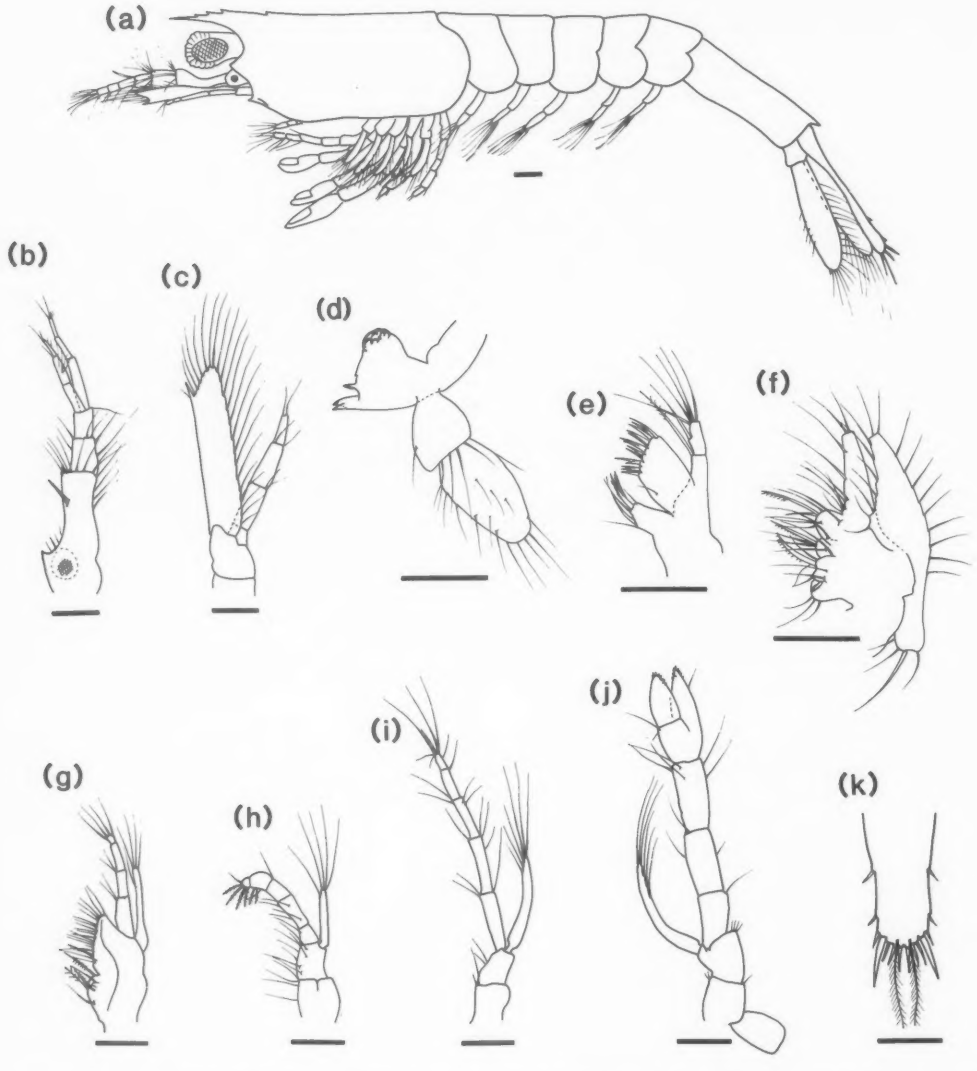

FIGURE 7.—*Atypopenaeus formosus* postlarva. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

Metapenaeopsis palmensis

The details of setation and segmentation for the various appendages are given in Figures 8 to 14 and in Table 2. The general development of *M. palmensis* parallels *A. formosus*, and only significant differences are given in the following text.

PROTOZOEA. Second antenna 0.7–1.0 times length of 1st antenna throughout protozoeal stage; 2nd antennal formula 1+2+2. Telson setal formula of 7+7 does not change until mysis II. Exopod of 2nd antenna bears 10 or 11 setae along its inner margin.

First substage (Table 2, Fig. 8a) with oval carapace bearing frontal organs and, above them, a prominent pair of pointed spines projecting forward between the 1st antennae. Length of these spines approximately equal to

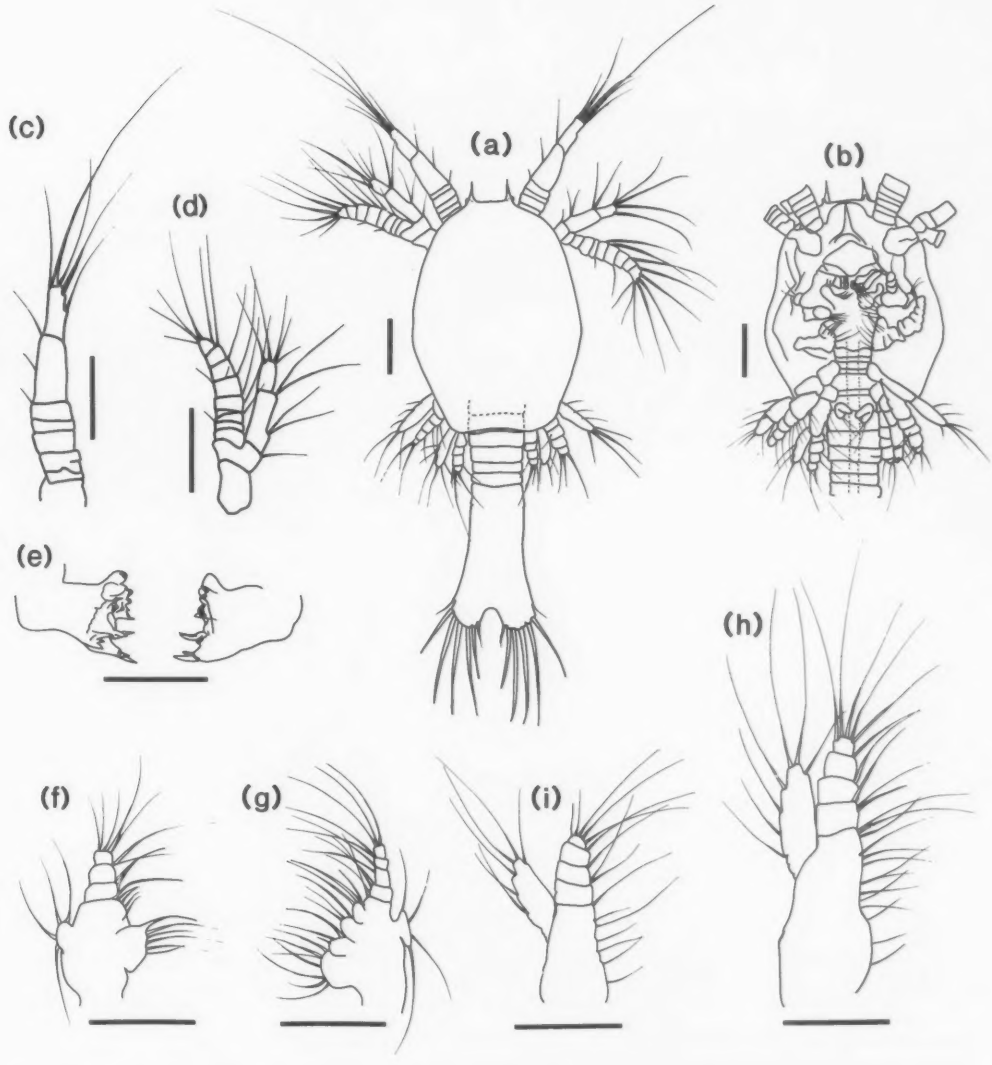

FIGURE 8.—*Metapenaeopsis palmensis* protozoea I. (a) whole animal, (b) ventral view of cephalothorax, (c) 1st antenna, (d) 2nd antenna, (e) mandibles, (f) 1st maxilla, (g) 2nd maxilla, (h) 1st maxilliped, (i) 2nd maxilliped. Scale = 0.1 mm.

diameter of basal segment of 1st antenna. Carapace length about half total length. Long labral spine (Fig. 8b). As in *A. formosus*, segmentation of 1st and 2nd maxillipeds variable and often indistinct (Fig. 8h, i). Second substage (Fig. 9) with long, down-curved rostrum extending beyond tip of eye. Two pairs of supraorbital spines. Both 1st and 2nd antennae stouter than *A. formosus* (Fig. 9b, c). In 3rd substage (Fig. 10) the inner supraorbital spines have almost disappeared, leaving only a protrusion in the carapace border or sometimes 1 or 2 small denticles (Fig. $10a_1$). Outer supraorbital spines remain distinct. Dorsal spines present on first 5 abdominal segments; lateral spines on 5th and 6th segments (Fig. 10a).

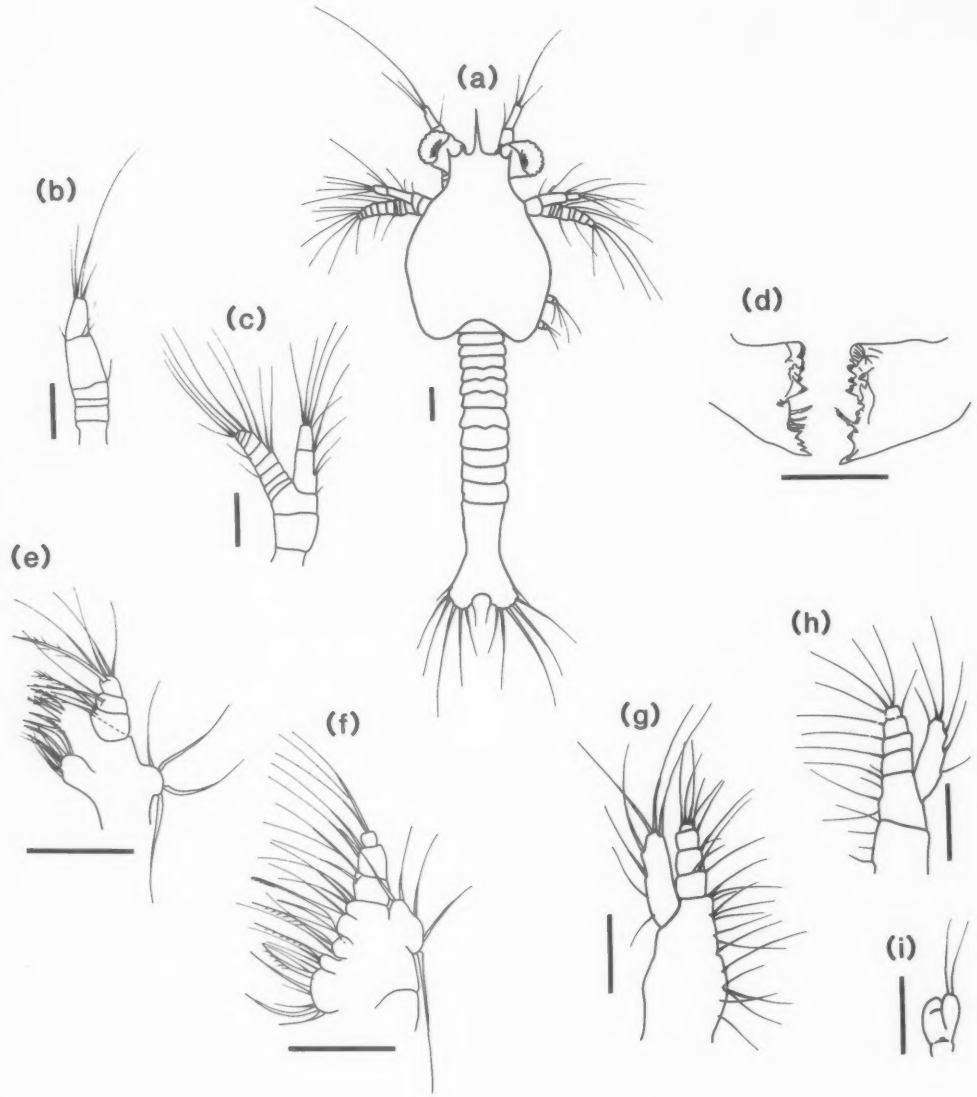

FIGURE 9.—*Metapenaeopsis palmensis* protozoea II. (a) whole animal, (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped. Scale = 0.1 mm.

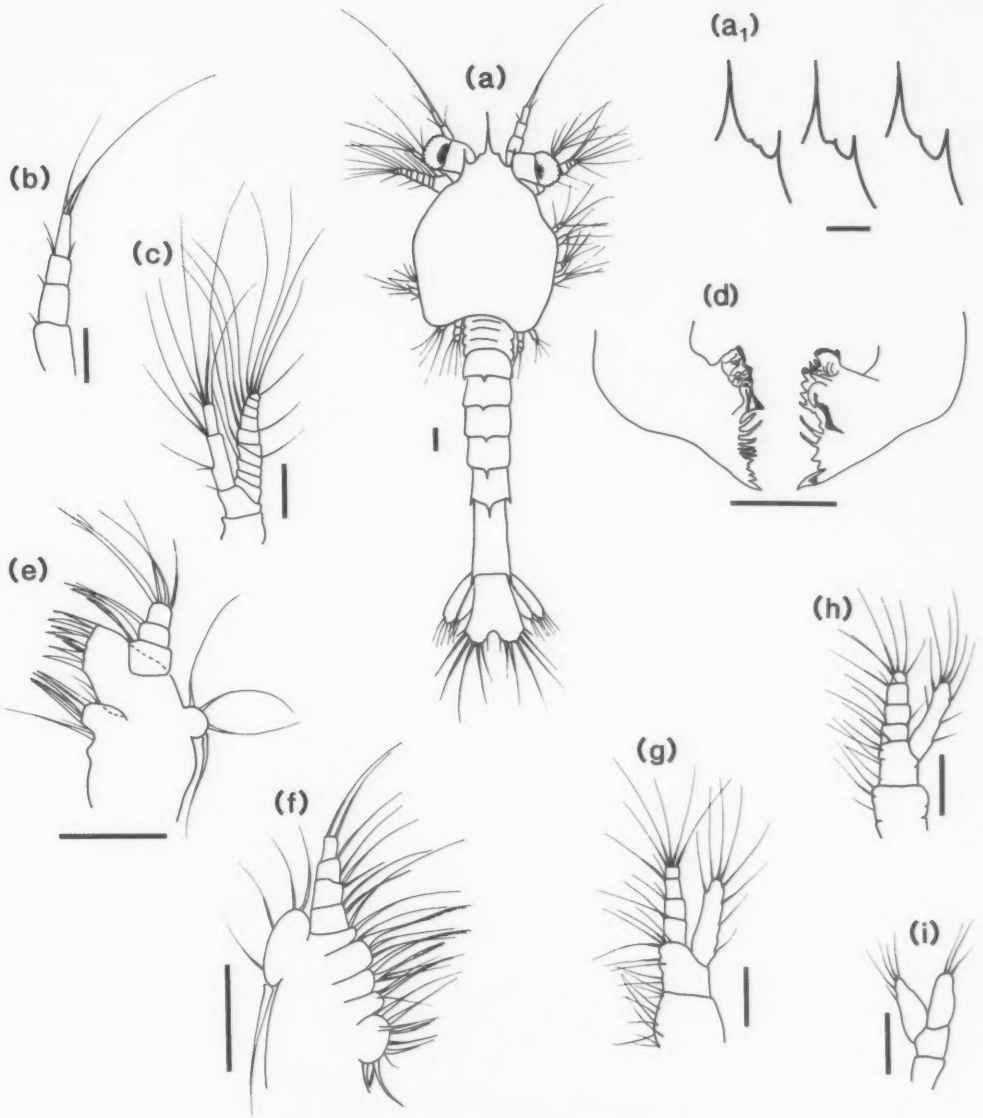

FIGURE 10.—*Metapenaeopsis palmensis* protozoea III. (a) whole animal, (a_1) detail – variation in form of inner supra-orbital spine rudiment, (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped. Scale = 0.1 mm.

MYSIS. In each substage, the carapace bears a distinctive series of spines or serrations along its anteroventral border (Fig. $11b_1$). The rostrum, down-curved, extends beyond eye. All mysis substages have supraorbital and pterygostomial spines. Small hepatic spine may be absent in 1st substage but always present afterwards. Dorsal spines sometimes on 4th abdominal segment, always on 5th and 6th, and lateral spines on 5th and 6th segments.

Mysis I of *M. palmensis* (Table 2, Fig. 11) retains 1 pair of supraorbital spines; rostrum has

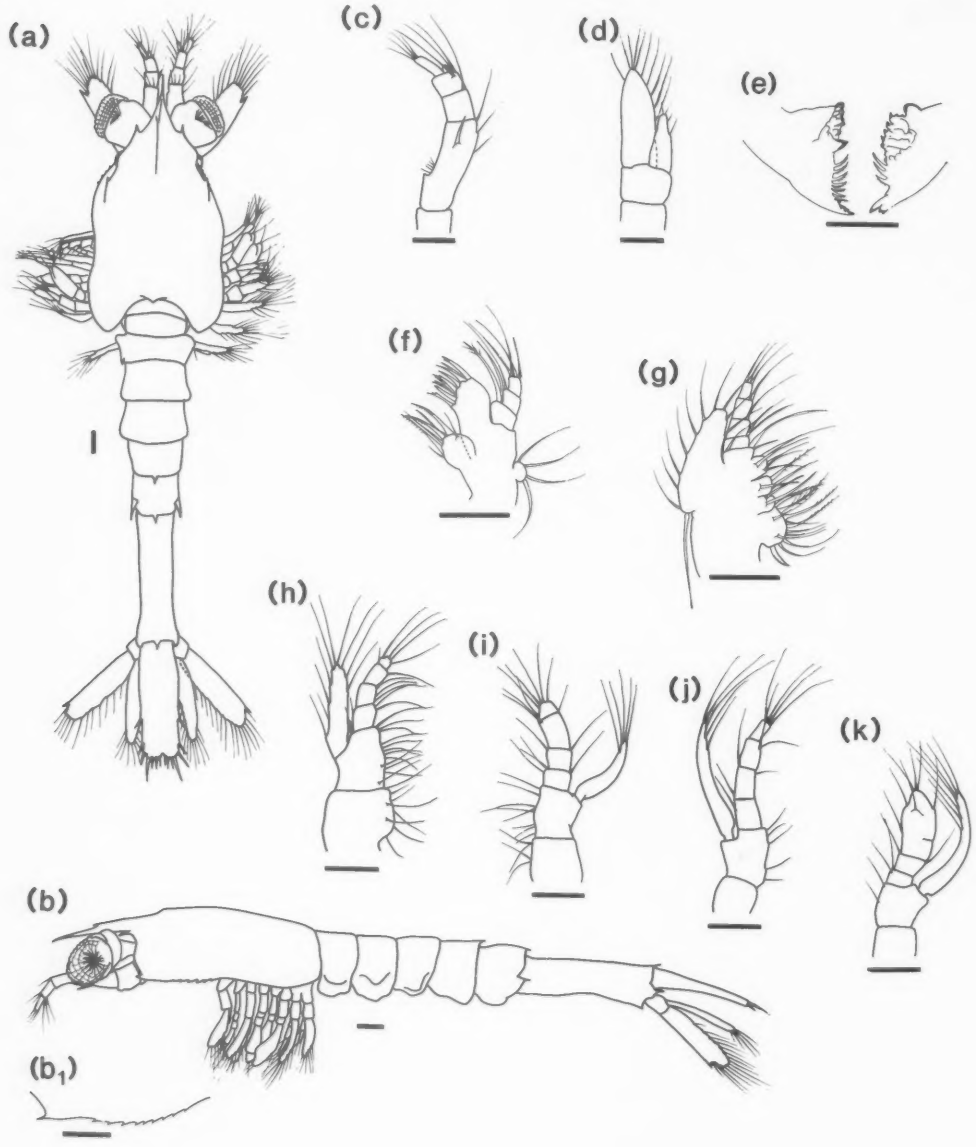

FIGURE 11.—*Metapenaeopsis palmensis* mysis I. (a) whole animal (dorsal view), (b) whole animal (lateral view), (b_1) detail-serrated anteroventral carapace margin, (c) 1st antenna, (d) 2nd antenna, (e) mandibles, (f) 1st maxilla, (g) 2nd maxilla, (h) 1st maxilliped, (i) 2nd maxilliped, (j) 3rd maxilliped, (k) 1st pereopod. Scale = 0.1 mm.

at most 1 dorsal tooth; small hepatic spine sometimes present (Fig. 11a, b). Epipod of 2nd maxilla (Fig. 11g) more enlarged than that of *A. formosus* at same substage. Mysis II (Fig. 12) with 2 dorsal rostral teeth, hepatic spine always present (Fig. 12a). In contrast to *A. formosus*, still no statocyst in 1st antenna (Fig. 12b), but 2nd antennal flagellum already as long as blade (Fig. 12c). Posterior border of telson with only slight cleft, and small median spine (telson formula now 7+1+7) (Fig. 12k). Mysis III (Fig. 13) with 2 or 3 dorsal rostral teeth and an epigastric tooth. First antenna now usually with a small statocyst (Fig. 13b); 2nd antennal flagellum longer than blade (Fig. 13c). Mandibles with unsegmented palp (Fig. 13d). Telson notch absent, posterior margin slightly rounded. Median spine still very short (Fig. 13k).

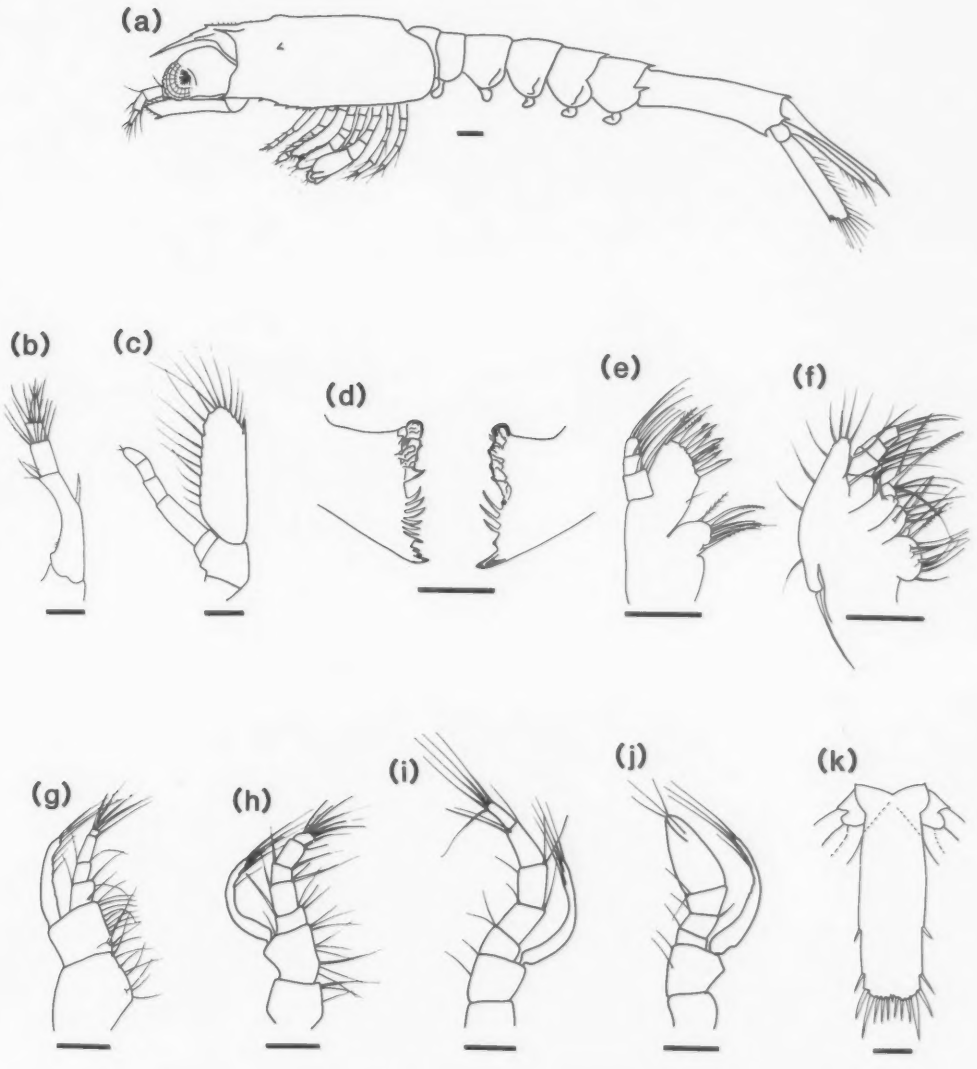

FIGURE 12.—*Metapenaeopsis palmensis* mysis II. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

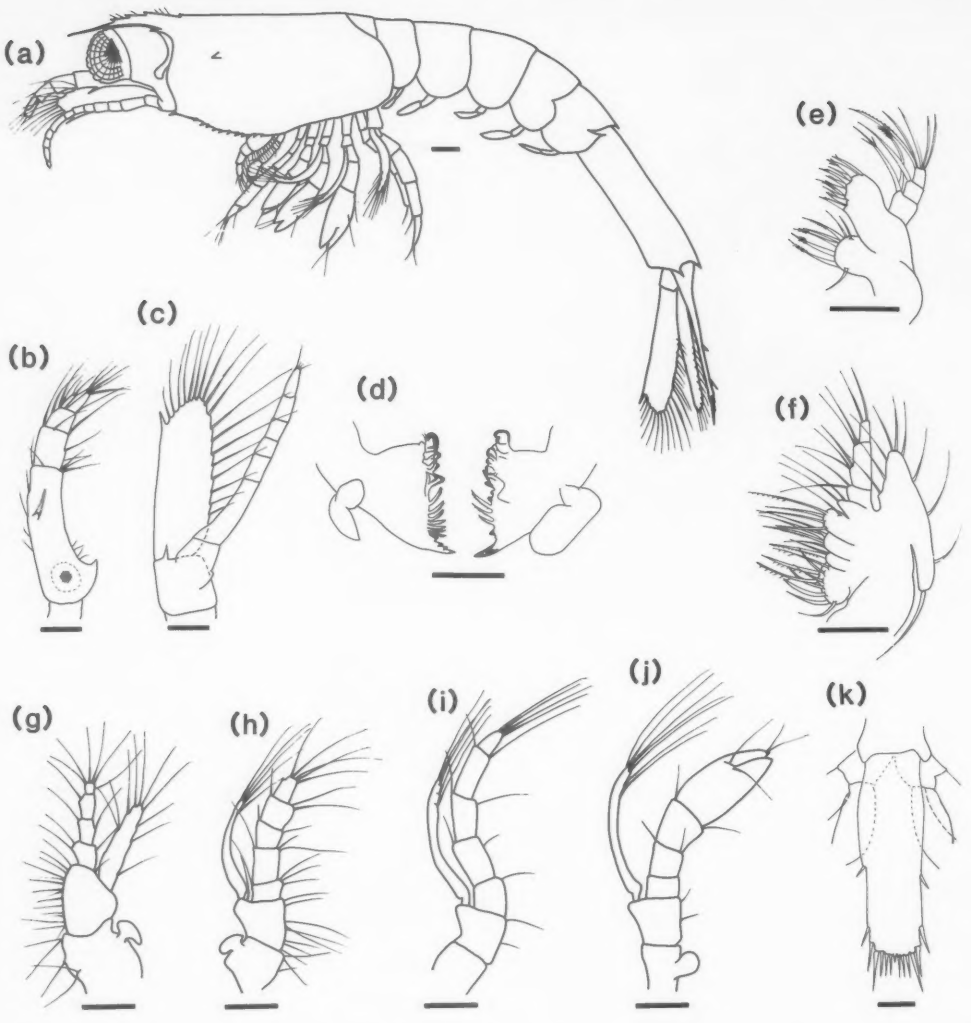

FIGURE 13.—*Metapenaeopsis palmensis* mysis III. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

POSTLARVA. The postlarva of *M. palmensis* (Table 2, Fig. 14) lacks the supraorbital spines and carapace serrations of the mysis substages. Pterygostomial spine and hepatic spine remain, now also a small antennal spine (Fig. 14a). Rostrum slightly shorter than eye, with 3 or 4 dorsal teeth and an epigastric tooth (Fig. 14a). First antenna lacking distal spine which *A. formosus* bears on proximal segment. Two small sternal spines on 1st thoracic segment, 2 long spines on 2nd thoracic segment (thoracic sternal spine formula 2+2+0+0+0) (Fig. 15d). Abdominal spination reduced, only 1 dorsal spine on 6th segment. Posterior margin of telson more V-shaped, spine formula remaining 7+1+7 (Fig. 14k). Median spine now large. Telson also bearing 3 or 4 small setae on each side of its posterior margin.

Generic Characteristics of Penaeid Larvae

The distribution of setae on the protopod and

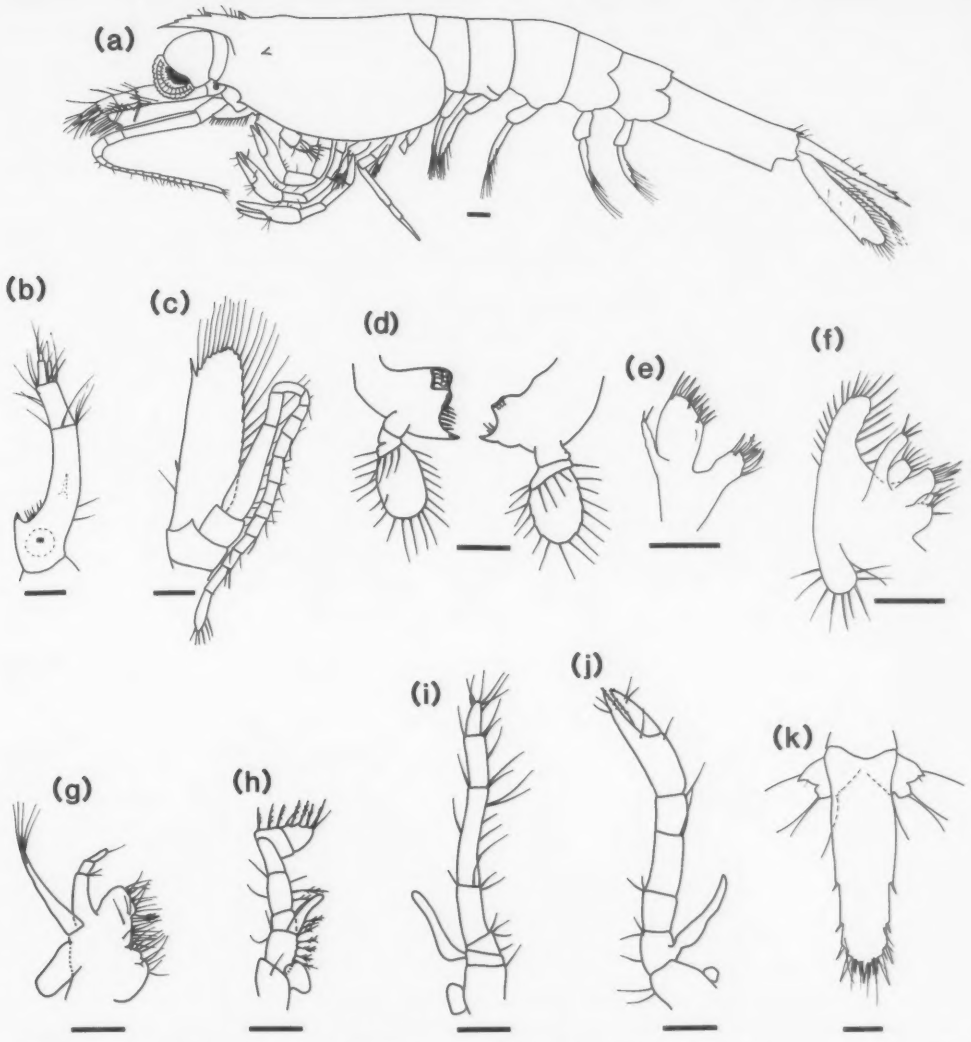

FIGURE 14.—*Metapenaeopsis palmensis* postlarva. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

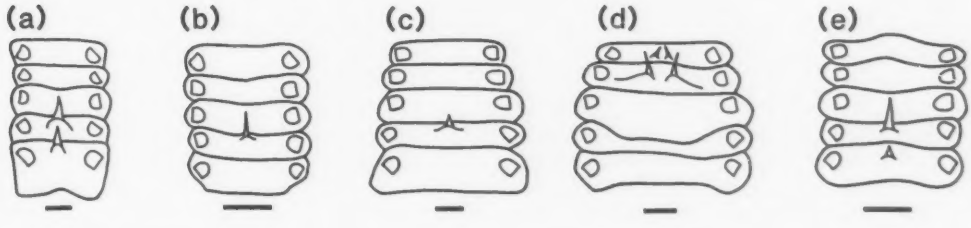

FIGURE 15.—Thoracic sternal spine distribution of postlarvae. (a) *Penaeus* (except for subgenus *Litopenaeus*; see text), (b) *Metapenaeus*, (c) *Trachypenaeus*, (d) *Metapenaeopsis*, (e) *Atypopenaeus*. Scale = 0.1 mm.

endopod of the 2nd antenna has been used for generic identification of protozoea (Cook 1966a; Hassan 1974; Haq and Hassan 1975). While this character is often referred to as the setal formula of the 2nd antennal endopod, this is not correct as the first seta referenced arises from the protopod.

We compared the 2nd antennal formulae of protozoeae in our reference collection with published formulae. All *Penaeus* larvae in our collection have the formula 1+1+2, in agreement with other published descriptions. The three species of *Trachypenaeus* in our collection (*T. anchoralis*, *T. fulvus*, and *T. granulosus*) have the formula 0+2+2, which is in agreement with the only existing published descriptions by Kirkegaard (1969) and Pearson (1939). *Parapenaeopsis* is represented in our reference collection by the protozoeae of *P. cornuta*, which also have the formula 0+2+2. This confirms the formula found by Hassan (1984) for *P. stylifera*. Rao (1973) also described larvae of *P. stylifera*, and his figures seem to indicate the same formula of 0+2+2, although no detailed drawings of appendages are provided.

However, the 2nd antennal formula is not consistent in all genera. There are five species of *Metapenaeus* in our reference collection: *M. bennettae*, *M. eborocensis*, *M. endeavouri*, *M. ensis*, and *M. insolitus*. These larvae normally have the formula 1+2+3, but on some occasions the formula is 1+2+2. This difference occurs at random (although rarely) among most species. Menon (1951), Morris and Bennett (1951), Raje and Ranade (1972), Kurata and Vanitchkul (1974), Courties (1976), and Hassan (1980) agreed that *Metapenaeus* have 1+2+2, while Vanitchkul (1970), Hassan (1974), and Haq and Hassan (1975) found both 1+2+2 and 1+2+3. In our larvae, the third seta in the most distal group was often small and hard to distinguish when present, and could easily have been overlooked. Similarly, the 2 species of *Metapenaeopsis* we have reared are not consistent. *Metapenaeopsis palmensis* is always 1+2+2, but *M. novaeguinae*, although normally exhibiting the same formula, occasionally has 1+2+3.

In the mysis stage, the presence of a serrate anteroventral carapace margin (Fig. 11b_1) is a character that has not previously been described for laboratory-reared penaeid larvae. At present the only genus in which it is definitely present is *Metapenaeopsis*—both *M. palmensis* and *M. novaeguinae* from our reference collection.

The number and placement of thoracic sternal spines have not been mentioned in previous studies. In cleared and stained specimens it is an easy character to assess and makes postlarval identification straightforward, and it is an important generic character in our key for postlarvae. Unfortunately these spines have not been described by other workers and so we have no information about the sternal spine formulae for genera that are not represented in our reference collection. Partly owing to this we have used other characters to help identify some genera; however, when both the size and position of the sternal spines are taken into account, they are sufficient to identify five genera: *Atypopenaeus*, *Metapenaeopsis*, *Metapenaeus*, *Penaeus*, and *Trachypenaeus* (Fig. 15). Within the genus *Penaeus*, the sternal spine formula has taxonomic value at the subgenus level. We have examined postlarvae from 3 species within the subgenus *Litopenaeus* (*P. setiferus*, *P. stylirostris*, and *P. vannamei*), all of which have only a single, small sternal spine on the 4th segment (formula 0+0+0+1+0). All other *Penaeus* examined have a large spine on the 4th segment and a small spine on the 5th (formula 0+0+0+1+1): *P. aztecus* from the subgenus *Farfantepenaeus*; *P. indicus* and *P. merguiensis* from the subgenus *Fenneropenaeus*; *P. japonicus* from the subgenus *Marsupenaeus*; *P. latisulcatus*, *P. longistylus*, and *P. plebejus* from the subgenus *Melicertus*; and *P. esculentus*, *P. monodon*, and *P. semisulcatus* from the subgenus *Penaeus*. Species of *Litopenaeus* do not occur in the Indo-west Pacific region and so will not be wrongly identified by our key.

We have not used the distribution of abdominal spines in protozoea III or mysis substages (e.g., Cook 1966a; Muthu et al. 1978), since their presence can be variable, at least for *M. palmensis*. Paulinose (1977) suggested that the dentition and asymmetry of the mandibles might be useful for both generic and specific identification of penaeid larvae. We have not investigated this possibility since the operational use of this character would not be practical due to the time-consuming dissections necessary.

Key to Penaeid Genera

Our key was constructed from both our own reference collection and published descriptions. Many species were referred to in characterizing the genera *Penaeus*, *Metapenaeus*, and *Trachypenaeus*. However, there is much less reference material available for other genera. Although

Metapenaeopsis has more species than any other penaeid genus found in the Indo-west Pacific region (Dall et al. in press), our key is based on just 2 species, both from our own reference collection. Characteristics of the genera *Atypopenaeus*, *Parapenaeopsis*, and *Parapenaeus* have been based on a single species. For this reason, and because the genera *Heteropenaeus*, *Trachypenaeopsis*, and *Penaeopsis* have been omitted, the key must be regarded as provisional, and subject to revision as more descriptions are published.

The protozoeae of *Metapenaeus*, *Atypopenaeus*, and *Metapenaeopsis*, and *Parapenaeus* are very similar. For protozoea II and III, distinction between these genera relies on the shape of the telson, rostrum, and supraorbital spines. These characters should be assessed with reference to Figures 17 and 18 and, if there is any doubt, the suite of characteristics in Table 3. In most cases the characters used in the key should be sufficient to identify mysis larvae and postlarvae without difficulty. However, as an additional check, the general shape of the antennal blades is a useful generic character, and should be compared with those shown (Fig. 16).

The family Penaeidae no longer includes members of the Aristaeidae, Solenoceridae, Sergestidae, or Sicyoniidae; these are now separate families within the superfamily Penaeoidea (Bowman and Abele 1982). We have restricted our key to the family Penaeidae. However, lar-

TABLE 3.—Characteristics of protozoeal stages of the genera *Atypopenaeus*, *Metapenaeopsis*, *Metapenaeus*, and *Parapenaeus*. Sources of information: *Atypopenaeus*, *Metapenaeopsis*, *Metapenaeus*—present study and reference collection of larvae held by the authors; additional sources for *Metapenaeus* species—see Dall et al. (in press) for review; specific sources referenced in table—*Parapenaeus stylifera* – [1]Heldt 1938, [2]Pearson 1939; *Metapenaeus monoceros* – [3]Courties 1976, [4]Raje and Ranade 1972.

	Atypopenaeus	*Metapenaeopsis*	*Metapenaeus*	*Parapenaeus*
Protozoea I				
Number of setae on 2nd antenna exopod inner margin	9-10	9-11	10	11
2nd antennal setal formula	1+2+2	1+2+2 or 1+2+3	1+2+2 or 1+2+3	0+2+2[1] or 1+2+2[2]
Anterior carapace	no spines	long spines	short spines except none for *M. ensis*, *M. monoceros*[3,4]	long spines
Protozoea II				
Number of setae on 2nd antenna exopod inner margin	9-10	9-11	10	11
2nd antennal setal formula	1+2+2	1+2+2 or 1+2+3	1+2+2 or 1+2+3	1+2+2[1] or 1+2+3[2]
Rostrum	longer than eye	longer then eye, curved	about eye length	longer than eye
Supraorbital spines	one	two similar size	one except for *M. ensis*, *M. monoceros*[3,4] (inner much smaller than outer)	two similar size
Protozoea III				
Number of setae on 2nd antenna exopod inner margin	9-10	10-11	10	11[2] or 12[1]
2nd antennal setal formula	1+2+2	1+2+2 or 1+2+3	1+2+2 or 1+2+3	0+2+2[1] or 1+2+3[2]
Rostrum	longer than eye	longer than eye, curved	about eye length	longer than eye
Supraorbital spines	one	one plus rudiment of second (Fig. 10a$_1$)	one	two (inner smaller than outer)
Telson spines	7+7	7+7	7+7	8+8

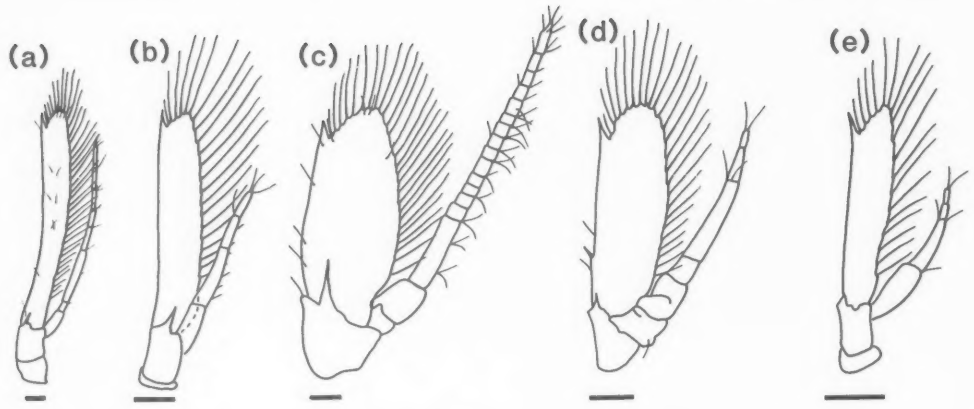

FIGURE 16.—Second antenna of postlarvae. (a) *Penaeus*, (b) *Metapenaeus*, (c) *Trachypenaeus*, (d) *Metapenaeopsis*, (e) *Atypopenaeus*. Scale = 0.1 mm.

vae from other families within the superfamily Penaeoidea might occur with penaeids. Characteristics that can identify larvae of related families are described by Cook (1966a) and Dall et al. (in press).

The key is not useful for later postlarval stages. It is difficult to define the cutoff point for older postlarvae, but the following characteristics may indicate that the postlarva is too old for accurate identification: there are more than 4 rostral spines; the antennal flagellum is longer than half the body length; the telson has a pronounced V-shape; and there are many setae on the telson.

Key

Protozoea

1 Setal formula on 2nd antennal protopod and endopod 1+1+2 ..... *Penaeus*
2nd antennal formula 0+1+2 ..... *Macropetasma*
2nd antennal formula not 1+1+2 or 0+1+2 2

2(1) 2nd antennal formula 0+2+2 3
2nd antennal formula 1+2+2 or 1+2+3 5

3(2) 2nd antennal exopod with 11 setae on inner margin ..... *Parapenaeus*
2nd antennal exopod with 10 setae on inner margin 4

4(3) Dorsal surface of carapace with small hump; telson notch moderately wide (Fig. 17c, i). ..... *Trachypenaeus*
Dorsal surface of carapace smooth; telson notch very wide (Fig. 17f, l). ..... *Parapenaeopsis*

5(2) Eyes immobile (protozoea I) 6
Eyes mobile (protozoea II or III) 9

Protozoea I

6(5) Strong spines above frontal organs, length at least 0.7 of 1st antenna diameter (Fig. 8a) ..... *Metapenaeopsis*
Spines above frontal organs small or missing 7

7(6) 2nd antennal exopod with 11 setae on inner margin ..... *Parapenaeus*
2nd antennal exopod with 10 setae on inner margin 8

8(7) Carapace about 0.5 of total length; usually small spines above frontal organs ..... *Metapenaeus*
Carapace about 0.4 of total length; no spines above frontal organs ..... *Atypopenaeus*

9(5) Uropods absent (protozoea II). 10

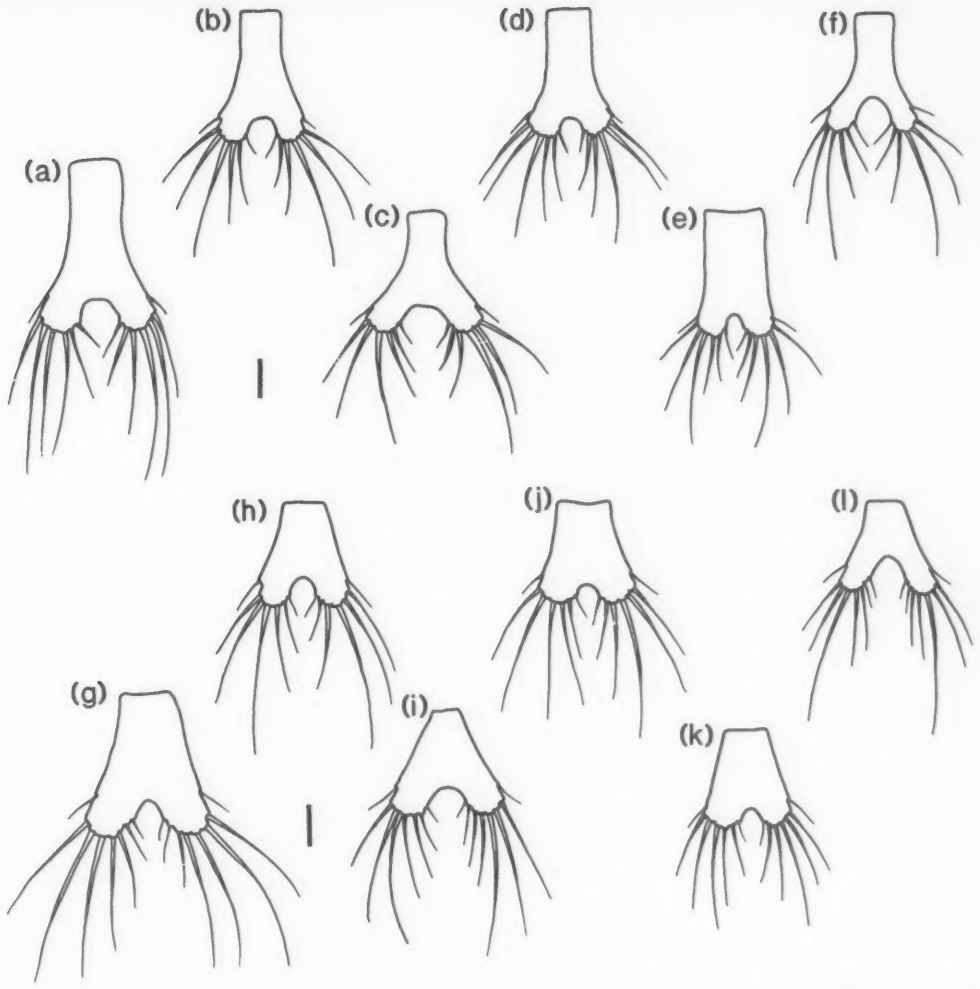

FIGURE 17.—Telson shapes of protozoeae. Protozoea II – (a) *Penaeus*, (b) *Metapenaeus*, (c) *Trachypenaeus*, (d) *Metapenaeopsis*, (e) *Atypopenaeus*, (f) *Parapenaeopsis*. Protozoea III – (g) *Penaeus*, (h) *Metapenaeus*, (i) *Trachypenaeus*, (j) *Metapenaeopsis*, (k) *Atypopenaeus*, (l) *Parapenaeopsis*. Scale = 0.1 mm.

Uropods present (protozoea III)..... 14

Protozoea II

10(9) A single pair of supraorbital spines (Fig. 2a)..... 11
Two pairs of supraorbital spines (Fig. 9a)..... 12

11(10) Telson wedge-shaped, with no distinct angle in lateral border (Fig. 17e)..... *Atypopenaeus*
Telson with a distinct angle in lateral border (Fig. 17b) ..... *Metapenaeus*

12(10) Inner pair of supraorbital spines filamentous and less than half as long as outer pair (Fig. 18)..... *Metapenaeus*[3]
Inner pair of supraorbital spines robust, similar in size to outer pair (Fig. 9a)..... 13

13(12) Body length greater than 1.6 mm .... *Parapenaeus*
Body length less than 1.6 mm..... *Metapenaeopsis*

[3] *M. ensis* or *M. monoceros*.

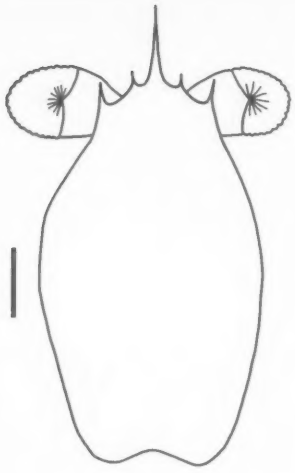

FIGURE 18.—Carapace of *Metapenaeus ensis* protozoea II. Scale = 0.1 mm.

Protozoea III

14(8) A single supraorbital spine, with straight carapace border between supraorbital spine and rostrum (Fig. 3a) 15
2 supraorbital spines, or 1 supraorbital spine with 1 or 2 small denticles, or a protrusion in carapace border between supraorbital spine and rostrum (Fig. $10a_1$) 16

15(14) Rostrum about same length as eye ... . *Metapenaeus*
Rostrum about 1.5 times eye length .. .. *Atypopenaeus*

16(14) Two well-defined supraorbital spines . ..... *Parapenaeus*
One supraorbital spine with 1 or 2 small denticles, or a protrusion in carapace border between supraorbital spine and rostrum (Fig. 10b) .... *Metapenaeopsis*

Mysis

1 Anteroventral margin of carapace serrated (Fig. $11b_1$) ..... *Metapenaeopsis*
Anteroventral margin of carapace smooth 2

2(1) 3rd abdominal segment with large dorsal spine; abdomen permanently flexed at 3rd abdominal segment (Fig. 19c) .. .. *Parapenaeus*
3rd abdominal segment with no spine or a small spine; no permanent flexion of abdomen 3

3(2) 5th abdominal segment with a large dorsal spine, equal in length to diameter of segment (Fig. 19a) .... *Macropetasma*
5th abdominal segment with no spine or with a spine of length less than half diameter of segment 4

4(3) Telson spine formula 8+8 5
Telson spine formula 7+7 7

5(4) Hepatic spine present ..... *Penaeus*
Hepatic spine absent 6

6(5) Rostrum very short, less than half eye length ..... *Trachypenaeus*
Rostrum longer than half eye length .. .. *Parapenaeopsis*

7(4) Rostrum down-curved, longer than eye ..... *Atypopenaeus*
Rostrum straight, shorter than eye... ..... *Metapenaeus*

Postlarva

1 3rd abdominal segment with large dorsal spine; abdomen permanently flexed at 3rd abdominal segment (Fig. 19d) ..... *Parapenaeus*
3rd abdominal segment with no spine or a small spine; no permanent flexion of abdomen 2

2(1) Rostrum with more than one dorsal tooth 3
Rostrum with zero or one dorsal teeth ..... *Macropetasma*

3(2) Telson with a median spine 4
Telson without a median spine 5

4(3) Telson with 8+1+8 spines .... *Parapenaeopsis*
Telson with 7+1+7 spines; thoracic sternal spine formula 2+2+0+0+0 (Fig. 15d) ..... *Metapenaeopsis*

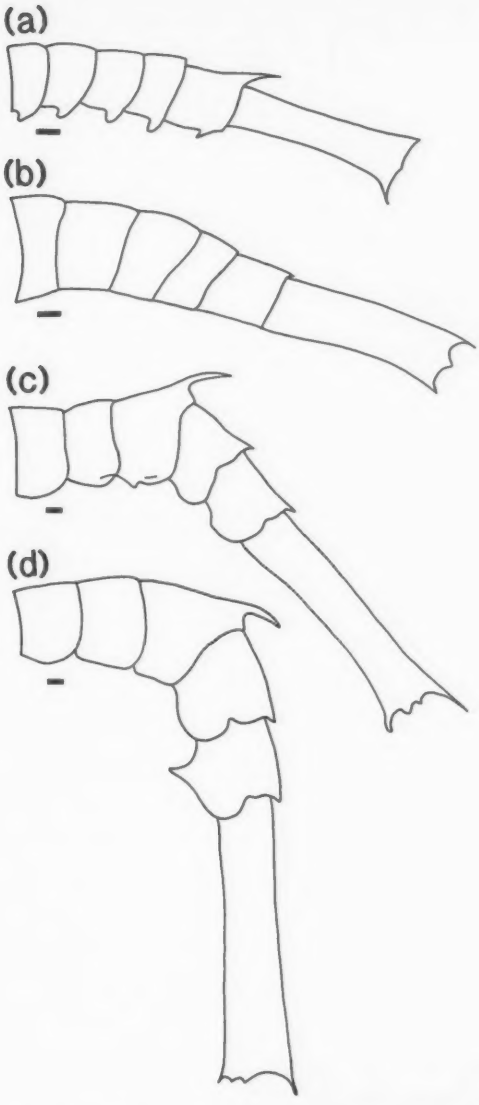

FIGURE 19.—Abdomen of *Macropetasma* (a) mysis II, (b) postlarva (redrawn from Cockcroft 1985) and *Parapenaeus* (c) mysis II, (d) postlarva (redrawn from Heldt 1938). Scale = 0.1 mm.

5(3) Telson with 8+8 spines 6
Telson with 7+7 spines 7

6(5) Thoracic sternal spine formula 0+0+0+1+1 (Fig. 15a) ..... *Penaeus*
Thoracic sternal spine formula 0+0+0+1+0 (Fig. 15c) ..... *Trachypenaeus*

7(5) Thoracic sternal spine formula 0+0+0+1+0 (Fig. 15b) ..... *Metapenaeus*
Thoracic sternal spine formula 0+0+0+1+1 (Fig. 15e) ..... *Atypopenaeus*

DISCUSSION

Previous Descriptions of Penaeid Larvae

The only way to describe the morphology and to be certain of the identity of penaeid larvae is to rear them in the laboratory, beginning with eggs from adults of known identity. Techniques for inducing penaeids to spawn and for culturing the larvae have been known for many years (Hudinaga 1942). For the genera *Penaeus* and *Metapenaeus* there are over 30 descriptions of larvae whose identity is certain (Dall et al. in press). Laboratory-reared larvae of other penaeid genera, also commercially important, are less well described. There are only a few useful descriptions of any species of *Parapenaeopsis* (Hassan 1984; Rao 1973), *Parapenaeus* (Heldt 1938; Pearson 1939) or *Trachypenaeus* (Pearson 1939; Kirkegaard 1969, protozoea I only), and this study is the first description of any species of *Metapenaeopsis* or *Atypopenaeus* based on laboratory-reared material.

Many workers have attempted to describe particular species or genera of penaeid larvae, based solely on planktonic material (see Dall et al. in press, for review). However the morphology of penaeid larvae undergoes major changes between each stage: egg to nauplius, nauplius to protozoea, and protozoea to mysis. Even between the protozoeal substages, changes are so great as to defy any attempt to link one substage with the next. A full larval life history cannot, we believe, be accurately reconstructed from larvae caught from the plankton unless at least some substages are subsequently reared (as in Pearson 1939).

The presence of commercial fisheries for a certain species is also a poor guide to the identity of larvae found in the same area. There may be significant populations of penaeid genera present that are not, for various reasons (small size, untrawlable habitat), represented in commercial catches. Larvae also have considerable potential for advection up to 150 km (Rothlisberg 1982; Rothlisberg et al. 1983b).

In several older studies, workers based their identification of larvae from the plankton on the temporal or spatial distribution of the adult

prawns, and were later found to be in error. For example, Heegard (1953) identified larvae from plankton collections as *Penaeus setiferus*. However, the protozoea I figured has a 2nd antennal setal formula of 0+2+2 and a wide telson notch, characters not seen in *Penaeus* but consistent with either *Trachypenaeus* or *Parapenaeopsis*. The protozoea II figured has the same 2nd antennal setal formula as the protozoea I, and the form of the rostrum and supraorbitals are not characteristic of *Penaeus*. However, this substage has supraorbital spines, which *Trachypenaeus* and *Parapenaeopsis* larvae do not. Heegard's protozoea III is consistent with *Penaeus* in some respects, such as the long rostrum, but its 2nd antennal setal formula is now 1+2+2, whereas the *Penaeus* formula is 1+1+2. It is likely that the protozeae described are from several genera, although the figures do not show sufficient detail for an accurate identification. On the other hand, Heegard's mysis figures are generally consistent with *Penaeus*, although the specific identification is in doubt since *P. aztecus*, *P. duorarum*, and *P. setiferus* all exist in the collection area. Similarly Dakin (1938) identified plankton-caught larvae as *P. plebejus*, but they were probably a combination of *Trachypenaeus* (based on the relative lengths of the 1st and 2nd antennae of protozoea III) and *Metapenaeus* (a 2nd antennal setal formula of 1+2+3 and telson with 7+7 spines in protozoea III). As a final example, Subramanyam (1965) reported a high density of penaeid eggs in the plankton off the Madras coast, and identified them as *P. indicus* after culturing several nauplius substages. However, the large egg diameter (0.45 mm) and large perivitelline space indicate that the eggs were probably *Trachypenaeus*, since *Penaeus* eggs have a diameter between 0.23 mm and 0.31 mm and a narrow perivitelline space (Dall et al. in press).

Descriptions of the lesser known penaeid genera from plankton samples may also be based on mistaken identifications. The only published description of larvae of the genus *Penaeopsis* is of *P. rectacuta* (Paulinose 1973), but the author gave no support for his choice of genus. The larvae were collected from areas of the Indian Ocean where species of other previously undescribed genera are common, including *Atypopenaeus stenodactylus*, *Metapenaeopsis andamensis*, *M. barbata*, *M. hilarula*, *M. mogiensis*, *M. philippii*, and *M. stridulans*, all of which are sufficiently abundant to support some commercial fishing (Dall et al. in press). The present description of *Metapenaeopsis palmensis* has much in common with several of the substages described by Paulinose (1973). The 2nd antennal formula of 1+2+2, a reduced second supraorbital spine in protozoea III, the rostrum length, the shape and spination of the mysis, and the serrate anteroventral carapace margin of the mysis substages are all consistent with *M. palmensis* described in the present study. Protozoea II is probably from a different genus, since it has no supraorbital spines [in all penaeids described except *Macropetasma africanum* (Cockcroft 1985) the presence or absence of supraorbital spines is the same for both protozoea II and III]. However, the figure of this substage shows the 2nd antennal exopod (on the whole animal) as symmetrical, with about 9 setae along both the interior and the exterior borders, whereas the drawing of the dissected appendage shows the more typical penaeid form of 10 setae along the inner border and 2 on the outer border. More subtle characters may also have been represented incorrectly, so confident identification is difficult; however, the characteristics shown (lack of supraorbital spines, a deep and wide telson notch and a relatively short rostrum) are consistent with both *Trachypenaeus* and *Parapenaeopsis*.

Paulinose (1986) described mysis I and II and an early postlarva (which, because of lack of setae on the pleopods, we call mysis III) from the Indian Ocean. He tentatively identified it as *Atypopenaeus stenodactylus*. However, these larvae resemble our *Metapenaeopsis palmensis* and differ from our *A. formosus* in the following important characters: rostrum length and shape (long and curved); the presence of a serrated anteroventral carapace margin; telson spine formula (7+7 for mysis I, 7+1+7 for mysis II and III) and abdomen spination (dorsal spines on the fourth, fifth, and sixth segments and lateral spines on the fifth and sixth segments). Although there are some differences between *M. palmensis* and the larvae described by Paulinose (1986), we feel that these larvae are not *Atypopenaeus* but most likely an unidentified species of *Metapenaeopsis*.

Most recently, Paulinose (1988) described mysis and postlarval stages of *Metapenaeopsis mogiensis*, *M. andamanensis*, and *M. barbata* from widely spread locations in the Indian Ocean. Unfortunately, genus and species were again assigned by comparison with known distributions of adult prawn species, and by linking substages based on similarity of appearance.

While the larvae have many similarities, there were two important characters missing from the *M. palmensis* described here, which Paulinose claims to be diagnostic for the genus: a dentate postero-inferior carapace margin, and serrated abdominal pleura. Given the large number of *Metapenaeopsis* species, these characters may vary within the genus.

Morphological Variation

The larval descriptions given in this study were based on a number of individuals sampled, where possible, from a number of spawnings. However, previous studies have shown that with the degree of intraspecific variation in morphology, hundreds of larvae from many spawnings should be examined, and each substage should be sampled several times to account for intramolt growth (Rothlisberg et al. 1983a; Jackson 1986). In this study, there was insufficient material for such exhaustive examination, and so the full range of variations may not be described.

Some morphological variation can be induced by environmental factors such as salinity and temperature (Jackson 1986), and the special environment of the laboratory may do the same. In an unsuitable laboratory environment, obvious deformities can occur (Rao and Kathirvel 1973), and less extreme environmental conditions may result in more subtle morphological effects. Therefore, while in this study much emphasis has been placed on laboratory rearing as a means of ensuring correct larval identification, more work is needed to discover to what degree laboratory-reared larvae differ from those in the natural environment. Differences between field-caught and laboratory-reared larvae have been found for the carid shrimp *Pandalus jordani* (Rothlisberg 1980), both in morphology and in the number of substages.

While many workers have searched for taxonomic characters to separate species of penaeid larvae within genera, they have generally been unsuccessful (Cook 1966b; Cook and Murphy 1971; Courties 1976). The only reliable way of distinguishing species of larval penaeids is to make a discriminant analysis of a number of morphological characters (Rothlisberg et al. 1983a; Jackson 1986). Discriminant analysis is less successful for postlarvae, and a technique based on electrophoresis is being developed (Lavery and Staples in press). The descriptions presented in this study are therefore of limited value in species identification.

Keys to the Genera of Larval Penaeids

The genera *Penaeus*, *Metapenaeus*, *Parapenaeopsis*, *Parapenaeus*, *Trachypenaeus*, *Metapenaeopsis*, *Atypopenaeus*, *Penaeopsis*, *Funchalia*, *Trachypenaeopsis*, *Sicyonica*, *Aristaeomorpha*, and *Solenocera* are included in Paulinose's (1982) key to penaeid larvae. Reconstructions of larval series from plankton collections were used as reference material for most of the genera. The protozoea key uses the length of the rostrum, the distribution of dorsal abdominal spines and the number of telson setae without qualifying these characters according to the substage. Most protozoeae would not be identified correctly because protozoea I does not have a rostrum; only protozoeae III have dorsal abdominal spines; and telson spines in *Penaeus*, *Trachypenaeus*, *Parapenaeopsis*, *Macropetasma*, and *Parapenaeus* vary in number between protozoea II and protozoea III. In the mysis key, *Atypopenaeus* are identified by a telson setal formula of 7+1+7, although the present study shows *A. formosus* has 7+7. *Metapenaeopsis* mysis larvae are said to have the pleura of the first five abdominal segments serrated ventrally, a characteristic not found in *M. palmensis* in the present study.

This is the first generic key for the Indo-west Pacific penaeid larvae that relies on descriptions of laboratory-reared larvae. Relying on laboratory rearings restricted the number of descriptions and species available for reference, but we feel this was justified by the improved precision obtained. In the present study, it was not possible to include *Funchalia*, *Heteropenaeus*, *Penaeopsis*, or *Trachypenaeopsis*, as no laboratory-reared larvae of these genera have been described. Owing to their rarity, the omission of three of these will have little effect on the practical application of the key. The fact that *Penaeopsis* is not included is more unfortunate since this genus is relatively abundant (Dall et al. in press). The key will be enhanced when larvae from the above genera are reared, as well as more species of *Atypopenaeus*, *Metapenaeopsis*, *Parapenaeopsis*, *Parapenaeus*, and *Trachypenaeus*. We have reared several species of *Trachypenaeus* and are preparing descriptions of *T. fulvus* larvae to compare with other *Trachypenaeus* species in our reference collection.

ACKNOWLEDGMENTS

Studying marine larval ecology and physiology is difficult: laboratory studies, requiring larval culture, are only now becoming routine, and field studies are fraught with taxonomic and sampling problems. Combined laboratory and field studies that provide real insight into the factors that affect larval distribution, abundance, and survival are that much more difficult and rare. Dr. Reuben Lasker and his group were pioneers and pre-eminent in this integrated approach. Taxonomic studies such as the present work are the basis for such research, which is only now beginning on tropical penaeids. We dedicate this paper to Reuben's inspiring example.

Many people assisted in larval rearing, including A. Chamberlain, R. Coles, P. Crocos, S. Frusher, D. Gwyther, G. Mawhinney, A. Ness, J. Salini, I. Somers, C. Tanakani, T. Wassenberg, and I. Zagorskis. Larval specimens were provided by M. Autrand, N. Hicks, H. Kurata, A. Lawrence, H. Motoh, J. Racovolis, L. Smith, and K. Yasuda. We also thank W. Dall, F. R. Harden Jones, V. Mawson, and D. Staples who provided helpful criticism of the manuscript.

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Larvae of *Liparis fucensis* and *Liparis callyodon*: Is the "Cottoid Bubblemorp" Phylogenetically Significant?

Jeffrey B. Marliave and Alex E. Peden

ABSTRACT: Larvae of the slipskin snailfish, *Liparis fucensis*, and of the spotted snailfish, *Liparis callyodon*, are described; and fecundity/spawning information for these species is provided. Positive identification of larvae of both species required that they be laboratory reared up to identifiable juvenile stages. Too little taxonomic information exists on larvae of this genus to reveal diagnostic characters for northeast Pacific species. The early development patterns of these two species are contrasted; *L. fucensis* larvae grow from a very small to a very large size during the larval stage, and develop an enlarged subdermal space, the "cottoid bubblemorph", whereas *L. callyodon* larvae develop more typically. Evidence from the literature indicates that this bubble morphology is a convergent, derived character, and is unsuitable for use in determining phylogenetic relationships.

Larval descriptions do not exist for any of the 17 species of the genus *Liparis* that occur in the northeast Pacific Ocean (Matarese et al. in press), except for illustrations of newly hatched *Liparis fucensis* (Marliave 1975). Larvae of the subfamily Liparidinae were discussed generally by Able et al. (1984), with emphasis primarily on pigment and ontogenetic schedule of developmental landmarks. Able et al. (1984) included an illustration (their figure 236 bottom) of an unidentified cyclopterid from southern California with an enlarged cranial and thoracic subdermal space giving a bubble appearance, and suggested that such a feature might be of taxonomic value. Another cottoid larva sharing this bubble appearance is *Malacocottus zonurus* (Washington et al. 1984). This type of anomalous morphological feature of a larval fish must be considered as a possible character for elucidating phylogenetic relations (Kendall et al. 1984), and the extent to which such a feature is conservative, as opposed to immediately adaptive, is fundamental to assessing the utility of such a feature as a phylogenetic character (Cohen 1984). Thus, Haeckel's biogenetic law, that ontogeny recapitulates phylogeny, becomes a moot theory with developmental stages as intensely subjected to selective pressures as the planktonic larval stages of fish. This paper provides insight regarding the presence (*fucensis*) versus absence (*callyodon*) of the larval cottoid bubblemorph in two closely related, sympatric *Liparis* species.

Adults of slipskin snailfish, *L. fucensis*, and spotted snailfish, *L. callyodon*, look very similar and are close in morphometrics and meristics (Clemens and Wilby 1961; Hart 1973). *Liparis fucensis* is distributed over a greater depth range than the shallow-water *L. callyodon* (Clemens and Wilby 1961); but they do overlap in shallow water. Spawning in *L. fucensis* involves the male tending egg masses deposited among polychaete worm tubes (Marliave 1975) or inside empty mussel shells (DeMartini 1978) in shallow subtidal waters. No information has been published previously regarding reproduction of *L. callyodon*.

Two different approaches for obtaining larval specimens—captive rearing and plankton towing—provided developmental series for these two species. Both species were reared through transformation to the juvenile stage, permitting positive identification. This paper provides the first larval descriptions for northeast Pacific *Liparis* species. The bubble morphology of *L. fucensis* larvae is constrasted with the more typical larval morphology of *L. callyodon*.

METHODS

Eggs and a 67 mm ripe male of *L. fucensis* were collected at a depth of 10 m from among the tubes of *Eudistylia polymorpha* by divers in Barkley Sound, British Columbia (lat. 48°50′N, long. 125°08′30″W) on 26 May 1974. The embryos were not visibly developed and the yolks were

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light orange in color. The eggs were incubated at 11°C and hatched on 10 June 1974. Larvae were held in static seawater without food and preserved at 0, 3, and 7 d posthatch. From April to July 1988, older larval stages were taken in epibenthic plankton tows in southern British Columbia, using a sled trawl with a 1.5 m × 0.8 m mouth and 1 mm mesh. The larvae were killed in the cod end bucket with anaesthetic and fixed in 5% formosaline. Several of the largest larvae were removed live and transported to a 1,000 L laboratory tank with through-flowing seawater of 10°C, where they were fed *Artemia* nauplii. Two individuals survived past settlement and were preserved as juveniles.

Unidentified eggs, later found to be *L. callyodon*, were collected from among barnacles and rock crevices in the intertidal zone (0.6 m above low water, Canadian scale) outside Sooke Basin in the Strait of Juan de Fuca (48°20′N, 123°44′W) on 22 March 1987 and 13 March 1988. In 1987, egg masses and newly hatched larvae were directly preserved. A variety of egg masses taken in 1988, ranging in color from maroon to orange to green, were incubated in inflow water of a 1,000 L through-flowing seawater tank and hatches occurred from late March through mid-April from the different masses. Larvae were fed *Artemia* nauplii that had been fed supplemental omega-3 fatty acids (Cooper 1988). Larvae were preserved from the rearing tank at various intervals up to the benthic juvenile stage.

Positive identification of laboratory-reared juveniles was based on the full spectrum of external juvenile characters from the literature (e.g., Hart 1973); larval characters alone could not be used to positively identify to the species level. Median fin ray meristics of late larval stages for these two species overlapped too broadly to permit positive identification prior to the juvenile stage. Juveniles used for identification of both species were deposited in the British Columbia Provincial Museum (BCPM 988-945, BCPM 988-946, BCPM 988-947, BCPM 988-948, BCPM 988-949).

Eggs and larval morphometrics were taken with vernier dial calipers under a dissecting microscope. Upon sorting, measures of notochord length (NL) or standard length (SL) were taken from fixed specimens. Body depth was measured near the pectoral base, where the maximum body depth dimension occurred, including subdermal space (i.e., dorsal epidermis to ventral epidermis). Body length was measured from tip of snout to posterior margin of anus, not including any portion of the abdominal cavity posterior to the anus. Pelvic disk width, not length, was measured. Too few specimens were available to permit clearing and staining, although quick-staining with alizarin red permitted viewing of external features. Illustrations were drawn using a dissecting microscope and camera lucida. Specimens of newly hatched *L. fucensis* from 1974, together with the photographs, permitted redrawing of an illustration from Marliave (1975).

Larvae of *Liparis fucensis*

Pigment intensity varied between siblings hatched in 1974. Similarly, larvae of like sizes and stage, which were captured from the field in 1988, varied in pigment intensity. The overall pattern did not vary much, although a few of the more intensely pigmented individuals tended to prematurely develop sets of melanophores that average larvae develop later. Also, these few intensely pigmented individuals developed a broader extent of particular pigment patches and more numerous, regularly spaced melanophores in rows along the anal fin base and ventral fin fold. Postflexion stages, in particular, tended to show a variation in extent or absence of pigment. Loss of early melanophores and appearances of different sets of melanophores seemed to characterize the postflexion period of development. Overall, however, pigment corresponded clearly to the distribution patterns and intensities illustrated in Figures 1 and 2.

At all stages, the epidermis had a noticeably granular appearance (Fig. 1), except around the outer margins of the tail fin fold. The final development of the expanded subdermal space, or bubble, corresponded to the extent of this granular appearance. On the largest preflexion larva, this granular layer could be scraped away from a basement membrane, on which melanophores remained.

Hatching occurred at 2.9 mm NL; the larvae had a prominent yolk sac with a single anterior oil droplet (Fig. 2a). At hatching, dorsal gut melanophores, about 20 postanal ventral midline melanophores, and a hexagonal honeycomb pattern of melanin on the pectoral fin bases were evident. At 10°C, yolk resorption occurred over a period of seven days under starvation conditions. During that time, larvae grew to 3.3 mm NL; head length increased from 19 to 21.5%

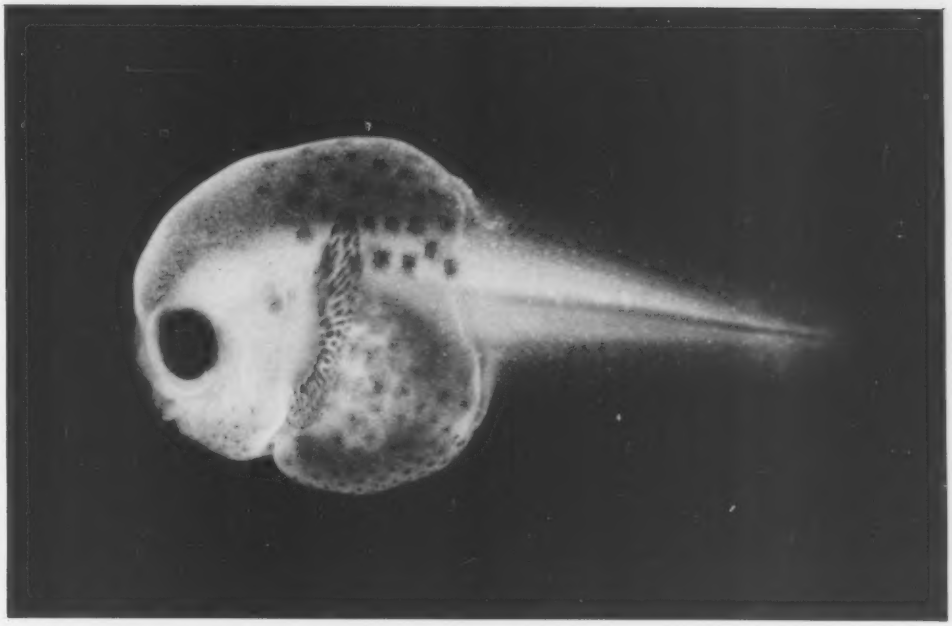

FIGURE 1.—Larva of *Liparis fucensis*, 6.9 mm NL preflexion. Note the granular appearance of the epidermis, visible especially in the cranial region, and the bubble shape of the expanded subdermal space.

NL, while snout-anus length remained at 38% NL. Body depth at yolk resorption was 27.6% NL, and the subdermal space had become prominent in the cranial area by this time. Pigment development during yolk resorption included the appearance of mandibular, ventral gut, and nape melanin, as well as a row of about 10 melanophores on the ventral margin of the fin fold. At hatching, the pectoral fin was only slightly larger than the eye; whereas, by yolk resorption it was 1.7 times as long and 2.3 times higher than the eye. It remained approximately this relative size through the remaining larval stages.

Through preflexion, relative head size increased largely through an increase in the bubble of the subdermal space. This bubble spread from the head region to include the nape and gut region. At 4.1 mm NL, snout-anus length had increased to 44% NL and body depth to 36% NL (Fig. 2b). The overall bubble appearance imparted by the subdermal space (see Figure 1) was evident by this stage, with the posterior margin of the bubble at the anus. Morphometric data on relative body depth and snout-anus length indicated that the development of the bubble is associated particularly with flexion (6–8 mm SL), the period of skeletal development. Just after flexion, a step-function increase in body depth and snout-anus length, relative to head length and standard length, marked the most rapid expansion of this bubble. Nostrils were prominently separated into dorsal and ventral nares by this stage. Through preflexion, pigment remained essentially the same as at the end of yolk resorption. Some preflexion larvae had up to 22 well-spaced, ventral, fin fold melanophores, and up to 24 postanal, ventral, midline melanophores. Such individuals also had denser mandibular melanophores, a few melanophores on the maxillary tip, and a few dorsal, midline melanophores posterior to the nape. Toward the end of preflexion, at 5.25 mm NL, the relative body depth had increased to 42%, and the snout-anus length, to 45%, giving the anterior body a nearly spherical bubble shape. At this size the position of the anus had become anterior to the posterior margin of the bubble portion of the subdermal space by two myomeres. The pelvic disk is not evident in preflexion larvae.

Late during the preflexion stage, larvae between 6 and 7 mm NL started forming dorsal and anal fin rays. These median rays started

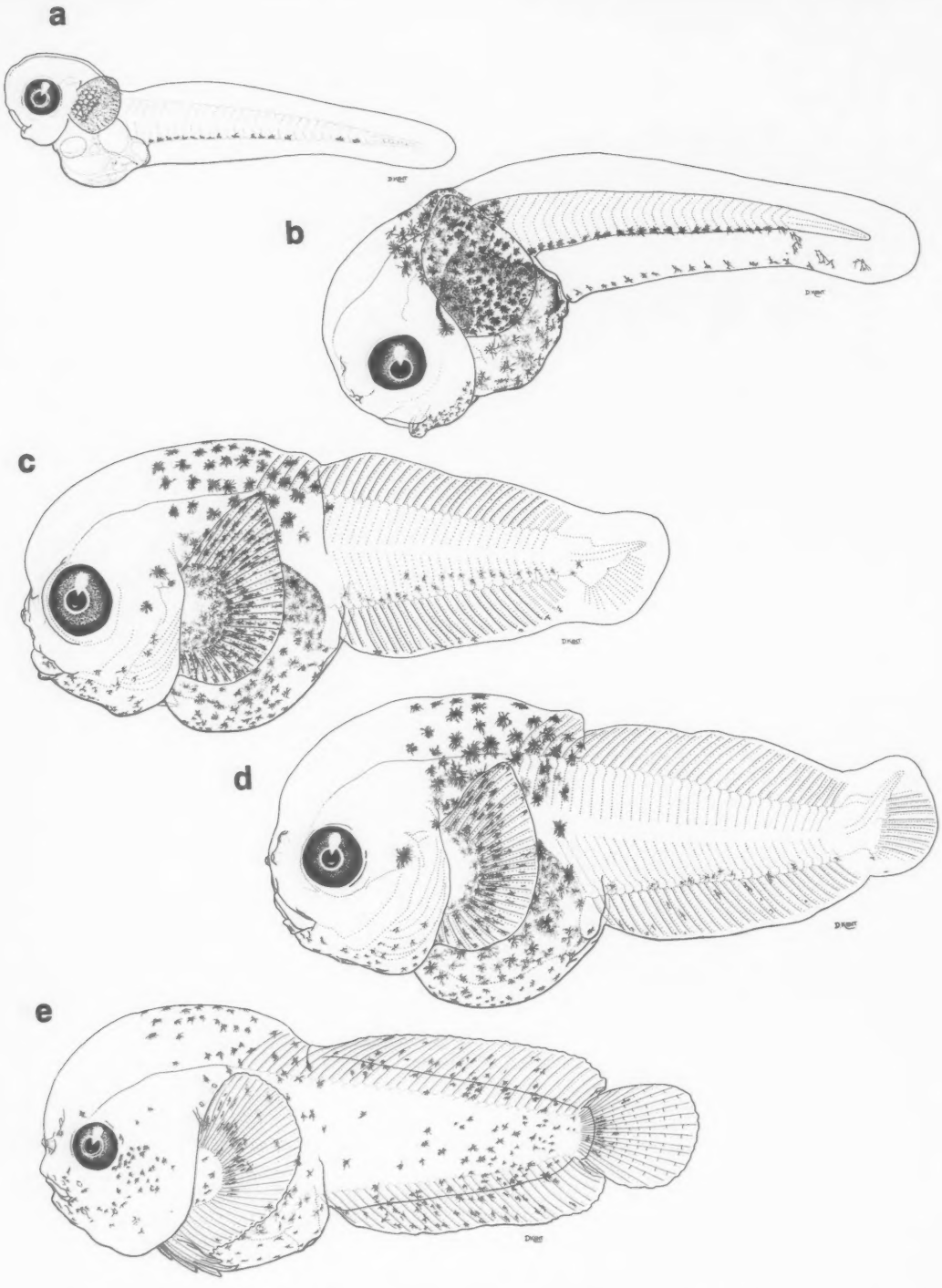

FIGURE 2.—Larvae of *Liparis fucensis*: a, 2.9 mm NL yolksac stage; b, 4.1 mm NL preflexion; c, 6.7 mm NL flexion; d, 8.7 mm SL postflexion; and e, 17.4 mm SL postflexion.

forming anteriorly, extending in decreasing length posteriorly. Pectoral rays were not evident in unstained material. Although the pectorals were very fully pigmented at this stage, the melanophores did not align with the underlying rays.

At the beginning of flexion, larvae between 6.7 and 7.3 mm NL developed dorsal, anal, and pectoral fin rays synchronously, prior to formation of caudal rays (Fig. 2c). Nape, gut, mandibular, and pectoral melanophores remained very prominent, with the addition of a few large melanophores in the opercular area. By this stage, the bubble was large and rather spherical, thus allowing epidermal melanophores to be distinguished readily from gut melanophores. The dorsal bubble melanophores around the nape were large and usually separated by a gap in epidermal pigment laterally, located in the plane of the large dorsal gut melanophores. The ventral bubble melanophores were markedly smaller by this stage, as were the mandibular melanophores. During flexion, postanal ventral, midline melanophores, particularly those in posterior positions, began migrating dorsally along the myosepta. Ventral fin fold melanophores eventually became aligned with the tips of anal fin rays.

During flexion, the final orientation of nares was attained, with the ventral naris on each side oriented anteriorly, and the dorsal naris, dorsally, and with the separation distance between the two nares of each pair similar to that of later stages, i.e., about 0.5 of eye diameter, slightly less than during preflexion. The pelvic disk was well developed and circular at this stage, slightly less than half of eye diameter in size. The pectoral fin did not extend ventrally to the pelvic disk, and no exserted lower rays were present.

During early postflexion, larvae up to 10 mm SL developed lower exserted pectoral rays but only in individuals in which caudal ray formation was completed (Fig. 2d). Early during postflexion, very small, mandibular, acousticolateralis pores became evident, three on each side. The pelvic disk was still small, embedded within an invagination of the bubble. The tail region formed a subdermal swelling, starting anteriorly, at sizes between 9 and 10 mm SL, extending out to under half the length of median fin rays.

Postflexion larvae tended to lose melanophores characteristic at earlier stages, while simultaneously developing new melanophores in other positions. Greater pigment variability between individuals was more evident at this stage than in earlier stages. All postflexion larvae lost the melanophores on the outer half of the pectoral fins, retaining rows of melanophores lining pectoral rays toward the fin base. A few individuals retained very small melanophores lining the fringe of the pectorals. These melanophores were frequently just on the dorsal tip of the pectoral fins, which tended to become less pointed via allometric reduction in ray length when the lower exserted rays formed. The exserted pectoral rays never developed pigmentation in larvae. Many individuals lost the small melanophores on the ventral bubble and mandibles, while the internal melanophores on the gut surface became obscured by the increasing thickness of the granular epidermis (cf. Fig. 1). Melanophores tended to develop along the margin of the tail swelling of the subdermal space, aligned with the midpoints of the dorsal and anal fin rays. At 16.8 mm SL (17.4 mm SL fresh, Fig. 2e), the outer skin was sparsely overlaid with melanophores everywhere except in the anterior cranial area. The melanin was most dense over the preopercular region and between the eye and the maxillary.

The largest postflexion larva, prior to the metamorphic allometry that yielded the juvenile morph, had tubular dorsal nares like the juveniles, but embedded in the bubble. The exserted, ventral, pectoral rays were the same length as the longest pectoral rays dorsally. The anterior portion of the dorsal fin was no longer visible within the bubble. Thus, only 25 posterior dorsal rays and 23 anal rays were evident. The mandibular, acoustico-lateralis pores were prominent and were aligned in a series of four on each side, extending toward the preoperculum. Two smaller pores were over the maxillary on each side. The pelvic disk had developed muscular papillae inside the margin; the shape was a flattened oval, with a width equal to the eye diameter.

The two larvae that survived to the juvenile stage in captivity underwent a metamorphic loss of the subdermal bubble. Over a period of nearly a month in the laboratory, the larvae were observed to show ambivalence between settlement and swimming in the water column. The pelvic disk was functional. Abruptly, the bubble appearance was lost on one juvenile that was observed at that stage; shrinkage occurred, giving the juvenile a slender, distinctively liparidine appearance. The other juvenile could not be

sighted until a later date when growth and deposition of intense dark pigment had occurred. Growth of the juveniles was very rapid compared with *L. callyodon*, as evident in Figure 2 versus Figure 3.

Larvae of *Liparis callyodon*

Preserved egg masses of *L. callyodon* numbered 409, 394, 203, 132, and 53 eggs (egg diameter 1.69 ± 0.02 mm, n = 10). Newly hatched *L. callyodon* averaged 5.21 ± 0.19 mm NL (n = 10). At hatching, snout-anus length averaged 39% NL (2.02 ± 0.16 mm); head length, 21% NL (1.08 ± 0.13 mm); body depth, 22.6% NL (1.18 ± 0.06 mm); and eye diameter, 9.5% NL (0.49 ± 0.02 mm). Pigment at hatching remained the same as in later preflexion stages (Fig. 3a) and consisted of large melanophores covering the entire body, except the posterior end of the notochord. There was also a row of elongated melanophores lining the ventral margin of the fin fold. At hatching, there was no pelvic disk, although the pectoral fin base extended ventrally toward the isthmus where the disk would form. The yolk included a single oil droplet, positioned anterodorsally within the yolk.

Considerable growth in size occurred during preflexion without any visible alteration in appearance (n = 17 specimens). Larvae less than 8 mm NL resembled the 5 mm yolk-sac larvae (Fig. 3). Pelvic disk width was about ⅓ eye diameter. At about 8 mm NL, growth in body depth occurred together with dorsal and anal fin ray formation; the rays formed synchronously along the entire fin lengths. In most specimens, dorsal and anal fin ray formation preceded both caudal and pectoral fin ray formation (Fig. 3b). Disk diameter was about ½ eye diameter at this stage. A few small melanophores had appeared in the dorsal fin area. The hypural primordia were present with no sign of notochord flexion. At lengths between 7 and 8 mm NL, morphometrics remained similar to those at hatching; the greatest changes were an insignificant increase in snout-anus length from 39 to 42% NL and a reduction in body depth from 22 to 19.5% NL.

Just beyond 8 mm NL, hypural plates formed at about the same time as pectoral fin ray bases. However, in a few specimens, these events just preceded anlagen of dorsal and anal fin rays, so the timing of these sets of events was very close and not entirely regular between individuals. At

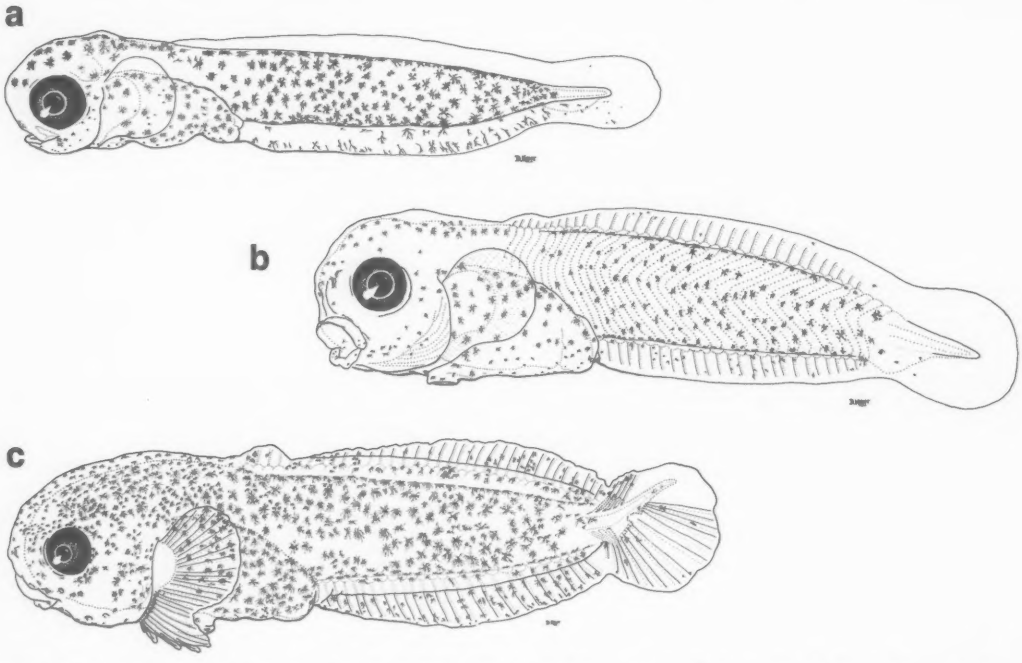

FIGURE 3.—Larvae of *Liparis callyodon*: a, 7.75 mm NL preflexion; b, 8.1 mm NL preflexion; and c, 10.45 mm SL postflexion.

a size of 8.8 mm NL, the hypurals were formed without caudal ray anlagen, and the pectoral fin ray bases were present. The anterior lobe of the dorsal fin (first dorsal) was becoming evident. The pelvic disk was only slightly smaller in diameter than the eye. At sizes between 9 and 9.9 mm NL, caudal rays formed, numbering 8 or 10 in different specimens, and pectoral rays developed from ½ to over ¾ of their length. All larvae under 10 mm NL were preflexion larvae. Larvae between 8.8 and 9.9 mm NL had the same morphometrics as smaller preflexion larvae, except a reduction from 9 to 7% NL in eye diameter.

Flexion occurred at sizes just beyond 10 mm NL, together with completion of caudal and pectoral fin ray formation. At 10.45 mm NL, the exserted lower pectoral rays were elongated, and the anterior lobe of the dorsal fin was becoming prominent. Disk width equalled eye width. Caudal pigment was forming, and the melanin on the rest of the body had become denser, although the pectoral fin remained unpigmented. The mandibular area was lined with 10 acousticolateralis pores (5 each side), and the maxillary region, with 8 pores. The nostrils were split into separate canals, with the ventral naris directed anteriorly in line with the eye pupil (about 66% pupil diameter) and with the dorsal naris directed up at a 45° angle to the level of the notochord (the opening half the diameter of the ventral naris). The cranial subdermal space was evident beneath the dense melanin. The operculum remained entirely open along the pectoral fin base and did not extend dorsally beyond the pectoral fin.

During postflexion (Fig. 3c), ambivalence between swimming and settlement became evident in the rearing tank (n = 3 individuals). Postflexion juveniles of about 12 mm NL had formed an acoustico-lateralis pore posterior to the eye, and two pores of the lateral line, immediately posterior to the dorsal end of the operculum. The operculum extended dorsally beyond the pectoral base, curving anteriorly as in adults. The opercular membranes with branchiostegals were fused with the isthmus up to about 7 rays from the top of the pectoral fin.

Juveniles of 20–22 mm SL showed different morphometrics from larvae: the snout-anus length was reduced from 42 to 36% SL; the eye diameter was further reduced to 5.7% SL; the head length increased from 21 to 24.4% SL; and the body depth slightly increased to 23.5% SL. In permanently settled juveniles at the largest sizes preserved, the opercular opening remained as low as the 4th or 5th pectoral ray; whereas, adult *L. callyodon* would not have this opening extending beyond the 1st ray (Hart 1973). The only other possible identifications from meristics were *L. cyclopus* and *L. florae*, but morphometrics, fin shape, and ecological information dictated against such determinations.

DISCUSSION

It must be reiterated that positive identification was, and now remains, possible only from juvenile material reared from known larvae. Future work may possibly permit identification from larval material for these Pacific *Liparis* species, but the present work serves only to focus such future efforts.

Taxonomic identification of *Liparis* species depends on numerous characters that are very difficult to determine in the smallest juvenile specimens. In addition, the opercular opening becomes smaller with development in *Liparis* species (Able et al. 1984). Therefore, rigid adherance to determining a restricted opercular opening size for identification of *L. callyodon* (cf. Hart 1973) should be expected to cause difficulty in identification of small juveniles. Further investigation of allometric reduction in opercular opening size in juveniles of the genus *Liparis* is required.

The fecundity (fewer than 400 eggs per mass) of *L. callyodon* was substantially less than the fecundity (about 1,500 to 5,000 eggs) determined for *L. fucensis* by DeMartini (1978). The average egg size, however, was larger at 1.7 mm for *L. callyodon* than for *L. fucensis* at 1 mm (Marliave 1975; DeMartini 1978). Adults of *L. fucensis* attain 30% greater maximum length than *L. callyodon* (Hart 1973). Furthermore, the *L. callyodon* egg masses collected, especially the counts of 132 and 53, may not have comprised the entire ovarian output of a female in every case because eggs were extruded into available interstitial spaces. This could sometimes restrict the number of eggs laid in one mass.

The larger eggs and apparent lower fecundity of *L. callyodon* resulted in considerably larger larvae at hatching than those for *L. fucensis*. Growth and development of *L. callyodon* occurred over a smaller range of lengths. Considering the cubic increase in volume with length for the bubblemorph of *L. fucensis* larvae, that unusual morph permitted enormous growth during the larval stage compared to the more typical *Liparis* larvalmorph of *L. callyodon*. Larvae of

L. callyodon resemble the few Atlantic species of *Liparis* that have been identified (Able et al. 1984), except for the unusually heavy melanization in larvae of this species. Intense melanization at hatching is more typical of cyclopterine than liparidine larvae (Able et al. 1984).

Although a relatively large subdermal space surrounding the entire body is typical of liparidine larvae, it is only as prominent as that illustrated in Figure 1 in *L. fucensis*, which may be the same species as that unidentified illustration previously referred to (by Able et al. 1984). That previously published illustration shows development of fin rays at a smaller size and with less melanin than in the present paper, but both of these features could result from the shrinkage and bleaching effects of long-term preservation. Another explanation for such differences is that regional differences might occur, as described for larvae of another cottoid species, *Oligocottus maculosus* (Marliave 1988). On the other hand, the unidentified illustration of a liparidine bubblemorph was drawn from a CalCOFI sample, which would be just south of the known range for *L. fucensis* (Hart 1973).

The larval bubblemorph of *L. fucensis* was collected in sled trawl tows taken within 1 m of the bottom at a wide variety of depths. In these same tows, larvae of Pacific whiting, *Merluccius productus*, were caught in the bottom tows at stages in which their swimbladder had developed, whereas earlier stages tended to be uniformly distributed through the water column (Marliave in press). Since cottoid fishes lack swimbladders at all stages, the evolution of a larval bubblemorph in the cyclopterid *L. fucensis*, in the cottid *Malacocottus zonurus* (Washington et al. 1984), and, to a less obvious extent, in the cottids *Gilbertidia sigalutes* and *Psychrolutes paradoxus* (Marliave 1975) may be an adaptation imparting neutral bouyancy, which would assist in maintaining a precise depth without costly swimming effort. The fluid of the subdermal space, if maintained at bodily osmolarity well below that of ambient seawater, would reduce overall density and lend to neutral bouyancy. Larvae possess swimbladders in certain other taxa that lack a swimbladder as benthic adults, as in the Gobiesociformes (Allen 1984); thus, the selective advantage of achieving neutral bouyancy appears to be relatively general among larval marine fishes.

Convergence toward the bubblemorph and midwater habitat is found in other genera. Most notably, Peden and Anderson (1978, 1979), Anderson (1977), and Peden (1979) discussed either the loose skin, which imparts a sort of bubble morphology, or the midwater habitat (i.e., neutral buoyancy) of the zoarcid genus *Lycodapus*. Anderson (1977, 1984) further noted that same habitat in *Melanostigma*, although this genus may possibly deposit demersal eggs in one species, *M. atlanticum*. Among liparidines, midwater habitat and bubble morphology are most specialized in *Nectoliparis* and *Liparicus*; these genera retain this specialized larval character into adult life (see Peden 1981 regarding midwater habitat). In these four genera, representing two distinctly divergent families with demersal ancestors, eggs producing relatively large and well-developed young are apparently deposited and reared, for most species, in the same midwater habitat as adults. In the case of the better known *Lycodapus mandibularis* (Anderson 1977; Peden and Anderson 1978; Peden 1979), adults are not known to select bottom habitat except accidentally during diel migration (Peden observation from submersible). Young, as small as 19 mm, are found in the same midwater tows as adults (maturity is at 75–90 mm in northern samples); owing to the large size of the eggs (Anderson 1977), the young are assumed to have hatched at relatively large sizes. Given the development of loose skin, or bubble morphology, in the more specialized and diverse genera of liparidines *Careproctus* and *Paraliparis* (Burke 1930; Stein 1978), many of which are from midwater, the bubblemorph, which originally evolved in a *Liparis*-like ancestor, has apparently been exploited in adult life histories of a large number of species. In some of these liparidine and zoarcid genera, some species may be associated with near-bottom habitats, and the bubblemorph may allow adults to hover just off the bottom similar to fishes with swimbladders (observed in *Lycodapus parviceps* by Peden from submersible).

The relatively neutral bouyancy that seems probable for the cottoid bubblemorph might permit relatively greater overall growth during the planktonic stage than for larvae of related species that have more typical larval morphology; e.g., larval *Gilbertidia sigalutes* grow to about 75% of their average adult size during the planktonic stage (Marliave 1981). This difference in larval growth seems to be the case for the present two *Liparis* species; the normal-type *L. callyodon* settles from the plankton at a very small size compared with the bubblemorph of *L. fucensis*. Bouyancy and potential growth rate

are both features that should be under immediate selective pressure; thus the presence or absence of the bubble morphology would be a derived character not suitable for revealing phylogenetic relationships.

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Development and Distribution of Larvae and Pelagic Juveniles of Three Kyphosid Fishes (*Girella nigricans*, *Medialuna californiensis*, and *Hermosilla azurea*) off California and Baja California

Elizabeth G. Stevens, William Watson, and H. Geoffrey Moser

ABSTRACT: Complete developmental series are described for larvae and pelagic juveniles of three kyphosid fishes, *Girella nigricans* (Ayres), *Medialuna californiensis* (Steindachner), and *Hermosilla azurea* (Jenkins and Evermann), from California and Baja California coastal waters. Larvae of the three species have a similar compact body form, with *G. nigricans* being the most slender and *H. azurea* the most robust. They share a number of pigment characters: including dorsal, ventral, and lateral midline melanophore series; an embedded melanistic band through the eye region; and minute melanophores at the tip of the notochord. Unique pigment variations permit the identification of all developmental stages of these species. Each has a specialized pelagic juvenile stage with distinct pigmentation. The pelagic distribution of each species is described; larvae of *M. californiensis* are the most oceanic and those of *H. azurea* the most coastal of the three species. The ontogenetic characters of these species are consistent with the view that they are monophyletic.

The opaleye, *Girella nigricans*, occurs from San Francisco, California, to Cabo San Lucas, Baja California. It is a prominent member of nearshore rocky reef and kelp communities from southern California to central Baja California and ranges from the intertidal zone to about 30 m depth. The halfmoon, *Medialuna californiensis*, occurs from Vancouver Island, Canada, to the Gulf of California, but is rare north of Point Conception, California. Its preferred habitat is similar to that of *G. nigricans*, although it ranges deeper to 40 m. The zebra perch, *Hermosilla azurea*, is known from Monterey Bay, California, to the Gulf of California but prefers warmer waters and is rare north of southern California. It is found in shallow inshore areas to a maximum depth of 8 m (Miller and Lea 1972; Feder et al. 1974; Eschmeyer et al. 1983).

Opaleye and halfmoon are part of the incidental catch of the coastal purse seine fleet and are sold as "perch" in the fresh fish market (Fitch and Lavenberg 1971). Annual landings of opaleye average about 2½ tons with a maximum of 12 tons in 1973; halfmoon landings average about 7 tons annually with a maximum of 25 tons in 1968 (Heimann and Carlisle 1970; McAllister 1975). Halfmoon are seasonally abundant in the southern California commercial passenger fishing boat catch, ranking as high as fifth in numbers caught (Crook 1978). They also consistently rank among the top 10 species caught by the southern California private sport fishery (Wine 1982). Fewer opaleye are landed in these fisheries, reflecting the shallower distribution of this species; however, opaleye are a mainstay for rocky-shore anglers in southern California and are the second most important species in competitive spearfishing events (Pinkas et al. 1968; Fitch and Lavenberg 1971). Zebra perch are taken occasionally by southern California shore anglers and spearfishers (Limbaugh 1955; Feder et al. 1974).

Knowledge of the early life histories of opaleye and halfmoon is scanty. They spawn during spring and summer and their larvae appear in nearshore plankton tows during this period. Both species have a silvery pelagic juvenile stage, and both appear in small schools in nearshore areas and around floating masses of kelp. Halfmoon continue their juvenile development in these habitats, whereas opaleye enter tidepools at about 25 mm length and change abruptly to olive colored individuals which have one or two white spots on the back, lateral to the dorsal fin. They remain in the intertidal region until about

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75 mm length when they begin to seek deeper subtidal habitats (Limbaugh 1955; Fitch and Lavenberg 1971; Kramer and Smith 1973; Feder et al. 1974; Gruber et al. 1982; Walker et al. 1987; Waples 1987; Waples and Rosenblatt 1987). Information on zebra perch is limited; their larvae occur in nearshore plankton tows in summer and fall (Walker et al. 1987) and small juveniles are reported to school with those of opaleye in August (Lockley 1952; Limbaugh 1955; Feder et al. 1974).

The systematic placement of these species is unsettled. Hubbs et al. (1979) and earlier workers recognized separate families for each of them, placing *G. nigricans* in Girellidae, *M. californiensis* in Scorpididae, and *H. azurea* in Kyphosidae; other workers have grouped the three species in Kyphosidae (Robins et al. 1980). Johnson (1984) maintained separate families for these species in his survey of percoid ontogeny and included two of our original drawings (10.9 mm *G. nigricans* and 10.1 mm *M. californiensis*) in his review.

The purpose of this paper is to describe the larvae and pelagic juveniles of *G. nigricans*, *M. californiensis*, and *H. azurea*, summarize their distributions from California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys and other sources, and point out ontogenetic characters that may be useful in defining systematic relationships.

MATERIALS AND METHODS

Larvae and pelagic juveniles of *G. nigricans* and *M. californiensis* were obtained principally from CalCOFI plankton surveys, while those of *H. azurea* came from nearshore plankton samples off the San Onofre Nuclear Generating Station (SONGS) (Barnett et al. 1984). Totals of 213 larvae and 111 pelagic juveniles were available for *G. nigricans*; 253 larvae and 31 pelagic juveniles for *M. californiensis*; and 79 larvae and 6 pelagic juveniles for *H. azurea*. Additional larval specimens of *G. nigricans* were obtained from a batch of field-caught eggs reared by David Kramer in the experimental aquarium of the Southwest Fisheries Center from 1 to 28 June 1968. We reared several batches of *G. nigricans* larvae from field collections of eggs in May to July 1978 and in July 1979. None of these larvae survived more than one week; however, they were useful in defining early pigment patterns.

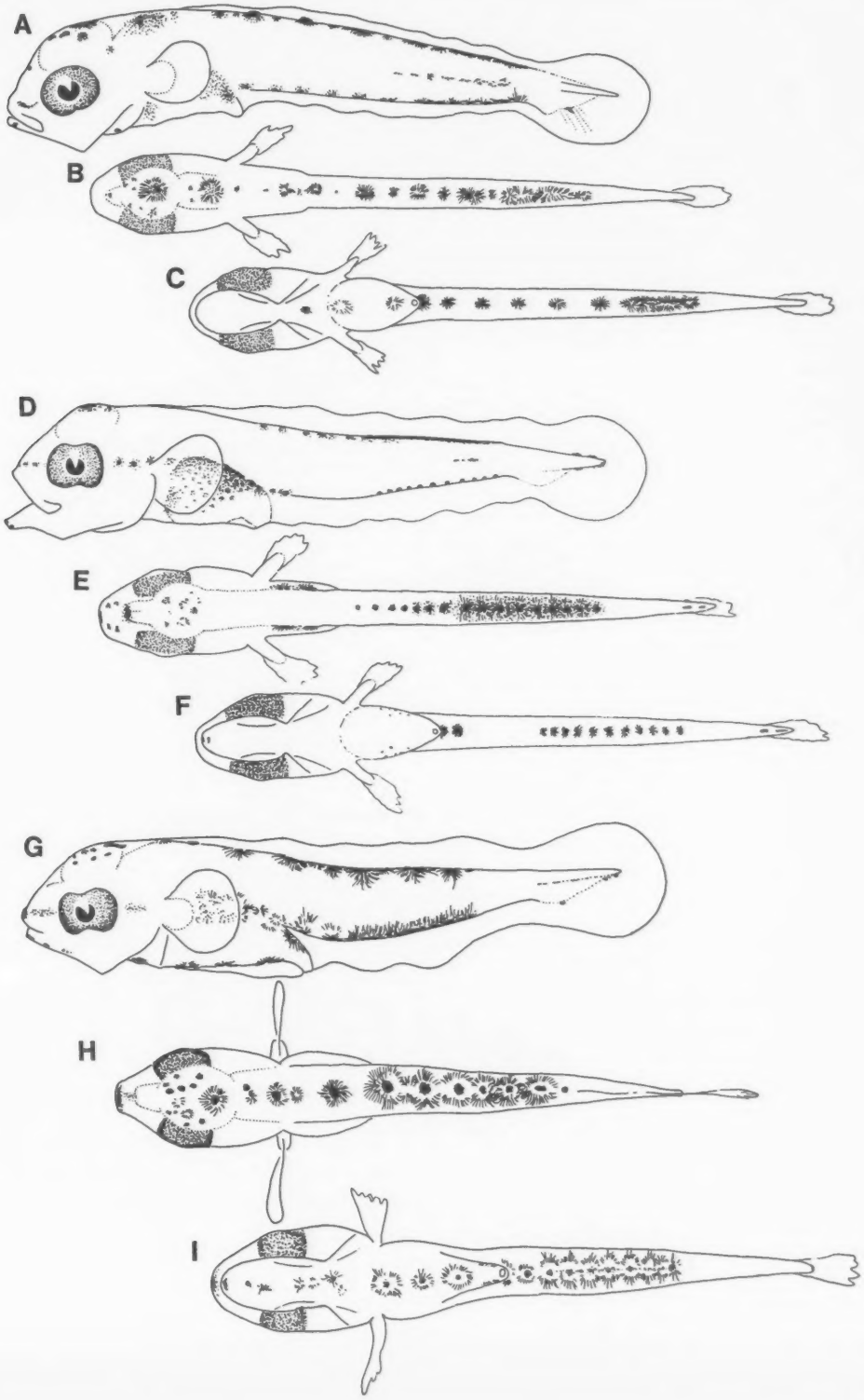
Developmental series were established to study general morphology, morphometry, and pigmentation; selected specimens were cleared and stained using the method of Potthoff (1984) to determine the sequence of ossification of fin rays, vertebrae, branchiostegal rays, and head spines. The descriptive methods and terminology follow Ahlstrom et al. (1976) and Johnson (1984). Prior to the completion of notochord flexion, body length was measured from the tip of the snout to the tip of the notochord and is designated notochord length (NL). In postflexion specimens body length was measured to the posterior edge of the hypural plate and is termed standard length (SL).

DISTINGUISHING FEATURES OF THE SPECIES

Larvae of the three species can be separated by melanistic pigment pattern (Fig. 1). Preflexion and flexion stage larvae of *G. nigricans* have one or two melanophores on the ventral midline of the gut. *Hermosilla azurea* usually have 3 or 4 (range, 1–6) evenly spaced melanophores in this region and *M. californiensis* larvae lack ventral gut melanophores during these stages. Preflexion and flexion larvae of *G. nigricans* and *H. azurea* have a series of evenly spaced melanophores along the ventral margin of the tail usually beginning at the first postanal myomere; in *M. californiensis* the series often is incomplete anteriorly (except in yolk-sac larvae). Larvae of *M. californiensis* usually have small melanophores dorsally and ventrally near the tip of the notochord. These melanophores are smaller, fewer, and often present only on the ventral margin in the other two species.

All three species are heavily pigmented along the dorsal and ventral margins through most of larval life and all three acquire a midlateral streak along the tail during notochord flexion. The streak originates more posteriorly in *M. californiensis* than in the other two species. In flexion larvae of *M. californiensis* and *H. azurea*, pigment spreads from the dorsal, lateral, and ventral series to form a band around the tail. This band originates more anteriorly

FIGURE 1.—Lateral, dorsal, and ventral views of early kyphosid larvae: (A–C) *Girella nigricans*, 5.7 mm NL, CalCOFI cruise 7805, station 90.28, surface tow; (D–F) *Medialuna californiensis*, 5.2 mm NL, CalCOFI cruise 6207–B, station 110.55, oblique tow; (G–I) *Hermosilla azurea*, 4.3 mm NL, MEC SONGS cruise I–80, surface tow.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and is broader in the latter species, although in both species it subsequently expands anteriorly to completely cover the sides of the body. Late larvae and pelagic juveniles of all three species are heavily pigmented; *G. nigricans* maintains a strong midlateral stripe, *M. californiensis* becomes uniformly pigmented, and *H. azurea* develops a mottled or barred pattern.

The three species differ in body depth, with *G. nigricans* the most slender and *H. azurea* the most robust. Developmental events occur at a smaller size in *H. azurea* than in the other species. Notochord flexion occurs between 4.1 and 5.8 mm in *H. azurea*, and between 5.8 and 8.6 mm in *G. nigricans* and *M. californiensis*. Transformation to pelagic juveniles occurs at about 11–12 mm in *H. azurea*, ca. 17 mm in *G. nigricans* and ca. 12 mm in *M. californiensis*. Head spination is more developed in *M. californiensis* than in the other two species.

Dorsal and anal fin ray counts are distinct for all three species at about 10 mm SL. *Hermosilla azurea* has XI, 11 dorsal rays and III, 10 anal rays while these fin formulas are D: XII–XIV, 12–15, A: III, 10–13 for *G. nigricans* and D: IX–X, 22–27, A: III, 17–21 for *M. californiensis* (Miller and Lea 1972).

Girella nigricans

Figures 1–3

General Morphology

Our smallest yolk-sac larvae are ca. 3.0 mm, have unpigmented eyes, a rudimentary mouth, and a large oval yolk sac which extends from the head to ca. midintestine and contains a single posteriorly located oil globule (ca. 0.16–0.20 mm diameter). Larvae are 3.5–3.7 mm long when the yolk is completely absorbed. Preflexion larvae are moderately slender with a relatively short coiled gut which extends slightly less than 40% of body length (Tables 1, 2). A small gas bladder is positioned anteriorly above the gut. The head is relatively small, with a blunt snout, and with round to slightly elongate (horizontally) eyes (Fig. 2).

Development is gradual during flexion and postflexion with no abrupt changes in body form or proportions. Most body parts increase relative to body length throughout the larval period with snout-anus length, head length, and body depth showing the greatest changes (Table 2). A small blunt spine develops at the angle of the preopercle in late preflexion larvae, and remains inconspicuous during later larval stages. No other head spines develop in larvae; however, one or more additional minute preopercular spines may appear in early pelagic juveniles. These specimens also develop an opercular and a minute supracleithral spine.

Notochord flexion begins at ca. 5.8 mm length and is completed by ca. 8.6 mm. Transformation into the pelagic juvenile stage is indicated by the appearance of scales (first seen in a 15.7 mm specimen), completion of fin ray elements, and attainment of juvenile pigment at about 17 mm (Fig. 3).

Fin Formation and Meristics

The first rays to calcify are the central principal caudal rays beginning late in the preflexion stage at ca. 5.8 mm (Table 3). The full complement of 9+8 principal rays is present midway through flexion and the procurrent rays begin to calcify at the end of flexion. The full complement of 10–12+9–10 procurrent rays is acquired in early pelagic juveniles (Table 3).

The dorsal and anal soft rays begin to calcify during flexion. Addition is posteriad with full complements attained in early postflexion. Dorsal and anal spines appear during early postflexion and are added in an anteriad direction. Full dorsal and anal fin complements (D: XII–XIV, 12–15; A: III, 10–13) are present in postflexion larvae 10.7 mm and larger.

The pectoral fins are initially rounded with rounded bases and retain this shape throughout the larval period; they become more elongate in pelagic juveniles. Calcification of rays begins midway through flexion; the upper rays are the first to appear and addition is ventrad. The full complement of 18–20 is present just before transformation into the pelagic juvenile.

The pelvic fins are the last to form. Fin buds appear midway through flexion and calcification of rays begins just after flexion is completed. The full complement of I,5 rays was present in specimens 10.7 mm and larger.

Initial vertebral ossification was not apparent in our stained series; however, the anteriormost 22 vertebral centra were already ossifying in a 6.7 mm larva. Ossification proceeds in a posteriad direction and the full complement of 27 vertebrae is present by the end of flexion. The branchiostegal rays begin to ossify late in preflexion and the full complement of six pairs of rays is present late in flexion.

TABLE 1.—Measurements (mm) of larvae and pelagic juveniles of *Girella nigricans*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Station	Body length	Snout-anus length	Head length	Head depth	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Predorsal length	Prepelvic length
6606–93.27	2.6	0.96	0.54	0.60	0.10	0.34	0.54	—	—	—	—
6307–83.39	2.7	0.86	0.51	0.44	0.08	0.28	0.46	0.14	—	—	—
8105–83.3.42	2.8	1.1	0.56	0.58	0.08	0.24	0.46	0.20	0.10	—	—
6606–93.27	2.9	1.2	0.65	0.74	0.09	0.22	0.60	0.20	0.10	—	—
8105–83.3.42	3.0	1.1	0.62	0.58	0.14	0.20	0.50	0.22	0.11	—	—
8105–83.3.42	3.1	1.1	0.64	0.64	0.16	0.20	0.56	0.30	—	—	—
6606–93.27	3.2	1.2	0.74	0.70	0.16	0.32	0.60	0.30	0.14	—	—
6509–120.40	3.4	1.4	0.45	0.48	0.11	0.26	0.45	—	—	—	—
6110–127.34	3.5	1.2	0.71	0.62	0.11	0.29	0.54	0.30	—	—	—
8105–83.3.42	3.6	1.2	0.72	0.66	0.12	0.26	0.60	—	—	—	—
SCBSIII 303	3.8	1.4	0.78	0.64	0.11	0.30	0.60	0.40	0.18	—	—
5710–123.37	4.1	1.8	1.0	0.80	0.22	0.34	0.79	0.60	0.22	—	—
SCBSIII 303	4.2	1.7	0.88	0.80	0.12	0.36	0.70	0.40	—	—	—
8105–103.3.29	4.3	1.8	1.0	0.80	0.22	0.42	0.78	0.46	0.18	—	—
5607–97.40	4.4	1.6	1.1	0.82	0.18	0.40	0.76	0.32	—	—	—
5708–127.34	4.5	1.8	0.86	0.84	0.23	0.33	0.80	0.44	0.16	—	—
8108–106.7.31	4.7	1.8	1.3	0.94	0.28	0.50	1.0	—	0.24	—	—
6310–87.32.5	4.8	2.0	1.2	0.96	0.24	0.42	0.84	0.60	0.22	—	—
6507–93.26	4.9	1.9	1.1	0.92	0.21	0.41	0.88	0.80	—	—	—
7805–90.28	5.8	2.0	1.4	1.1	0.32	0.52	1.0	0.60	0.36	—	—
5910–127.34	6.0	2.3	1.5	1.3	0.40	0.54	1.2	0.60	0.36	—	—
8107–83.3.42	6.1	2.3	1.5	1.2	0.36	0.56	1.3	0.60	0.34	3.2	—
8105–103.3.29	6.2	2.3	1.6	1.2	0.24	0.60	1.2	0.60	0.42	3.2	1.8
7805–90.28	6.3	2.4	1.5	1.2	0.36	0.60	1.2	0.64	0.36	3.3	—
8105–103.3.29	6.4	2.5	1.7	1.1	0.42	0.56	1.1	0.80	0.36	3.4	—
7805–90.28	6.5	2.3	1.6	1.2	0.32	0.60	1.2	0.88	0.40	3.3	1.5
8107–93.3.50	6.6	2.6	1.4	1.4	0.34	0.66	1.4	1.0	0.50	4.0	2.1
8107–93.3.50	6.7	2.7	1.8	1.5	0.46	0.72	1.5	0.80	0.30	3.7	2.1
7805–90.28	6.8	2.5	1.8	1.3	0.34	0.62	1.3	0.60	0.32	3.8	2.0
7805–90.28	7.0	2.8	1.9	1.4	0.40	0.68	1.4	0.82	0.40	4.0	2.0
7805–90.28	7.1	2.8	2.0	1.4	0.42	0.68	1.4	0.76	0.56	3.9	2.0
8105–103.3.29	8.2	3.6	2.4	1.7	0.48	0.88	1.8	1.1	0.42	3.8	2.7
8107–80.51	8.4	3.8	2.4	1.7	0.40	0.84	1.7	0.92	0.54	4.8	2.5
8105–86.7.35	8.6	3.7	2.5	1.8	0.60	0.88	1.9	1.2	0.56	4.0	2.8
8105–86.7.45	8.6	4.0	2.8	2.1	0.60	0.88	2.2	1.2	0.70	3.8	2.9
8105–86.7.33	10.7	5.5	3.1	2.2	0.64	1.1	2.5	—	0.68	3.9	3.4
7803–90.60	11.9	5.7	3.3	2.0	0.74	1.2	2.5	1.8	0.68	3.8	3.8
8108–96.7.35	14.8	8.1	4.9	3.8	1.0	1.6	3.8	2.6	0.80	5.7	5.2
8107–93.3.55	15.8	8.5	5.0	3.4	1.2	1.5	3.8	3.2	0.92	5.2	5.2
8107–93.3.55	16.5	8.3	5.2	3.7	1.2	1.6	4.1	2.8	1.0	6.0	6.0
8107–80.55	17.3	9.2	5.5	3.7	1.3	1.8	4.2	3.3	1.2	5.8	5.7
8108–103.3.30	18.4	10.3	5.8	4.5	1.5	1.8	5.0	3.4	1.2	6.8	6.7
8102–120.30	19.5	10.8	5.8	4.6	1.4	1.8	5.1	4.8	1.2	6.9	6.4
6612–123.36	23.2	12.0	6.9	5.8	1.8	2.2	6.7	5.0	1.6	8.2	7.7

TABLE 2.—Average body proportions (% ± standard deviation) for larvae of

Species/stage	Snout-anus length / Body length	Head length / Body length	Head depth / Body length	Snout length / Body length	Eye diameter / Body length
Girella nigricans					
Preflexion	38.2 ± 2.92	21.5 ± 3.07	19.3 ± 2.49	4.1 ± 1.06	8.7 ± 1.58
Flexion	38.9 ± 2.91	25.8 ± 2.15	19.8 ± 1.35	5.6 ± 0.82	9.6 ± 0.60
Postflexion	49.6 ± 4.15	30.7 ± 2.05	21.8 ± 2.88	6.8 ± 0.57	10.1 ± 0.42
Juvenile	54.1 ± 1.99	30.7 ± 1.13	23.6 ± 1.57	7.7 ± 0.43	9.7 ± 0.51
Medialuna californiensis					
Preflexion	39.6 ± 2.49	21.2 ± 3.23	19.1 ± 2.09	4.1 ± 1.23	8.4 ± 0.64
Flexion	44.3 ± 4.31	27.2 ± 3.88	21.8 ± 2.21	6.3 ± 0.86	10.7 ± 1.15
Postflexion	50.6 ± 4.13	30.5 ± 3.29	23.3 ± 1.46	6.0 ± 0.75	10.8 ± 0.33
Juvenile	56.5 ± 2.29	33.4 ± 1.75	27.2 ± 2.05	6.7 ± 0.92	10.6 ± 0.70
Hermosilla azurea					
Preflexion	51.0 ± 3.23	28.4 ± 3.10	23.5 ± 3.31	6.1 ± 1.66	11.0 ± 0.47
Flexion	54.2 ± 3.06	31.9 ± 3.90	24.0 ± 3.42	7.9 ± 1.46	11.6 ± 1.06
Postflexion	57.3 ± 1.03	31.7 ± 2.25	25.8 ± 1.72	7.5 ± 0.55	12.2 ± 0.75
Juvenile	58.0 ± 1.83	32.8 ± 1.89	25.8 ± 2.06	6.5 ± 0.58	11.2 ± 0.96

Pigmentation

Pigmentation of yolk sac and early preflexion larvae was described by Orton (1953) from specimens cultured in the laboratory. Newly hatched larvae have a few melanophores on the hindgut and in a short midventral row at the base of the tail. At about midway through yolk absorption, small melanophores appear on the ventral surface of the yolk sac (Fig. 2A); the row above the hindgut becomes heavier, extending forward to about the midpoint of the yolk sac; and the midventral tail series has increased to 7–11 melanophores, extending posteriad along most of the tail. A series of small melanophores appears on the dorsal midline along the posterior half of the tail, and several small melanophores are present above and below the tip of the notochord. Near the end of yolk absorption the eyes become pigmented; the dorsal gut pigment becomes heavier and extends over the entire gut; and the ventral tail melanophores enlarge, partly by aggregation, as do the melanophores on the dorsal margin of the tail.

In early preflexion larvae the ventral midline series of 5–8 large melanophores is continuous with the dorsal gut melanophores. A space separates the ventral tail series from one or more smaller melanophores near the tip of the notochord. The dorsal midline series consists of ca. 1–4 large melanophores posteriorly on the tail, with one to several small melanophores near the tip of the notochord. A large melanophore develops above the midbrain and one forms on the nape. Internal pigment develops below each otic capsule, appearing as a continuation of the dorsal gut pigment. The series of small ventral gut melanophores coalesces into 3 pigment loci, each usually containing a single melanophore: 1) an embedded melanophore anterior to the liver, 2) a surface midventral spot just posterior to the liver, 3) a surface midventral spot just anterior to the hindgut (Fig. 1C).

During preflexion the dorsal gut pigment expands to the lateral surface of the gut. The dorsal midline series increases anteriorly beginning in early preflexion, and soon extends from the head nearly to the tip of the tail. The smaller melanophores near the tip of the tail disappear or are reduced to one. Dorsal melanophores number 11–15. The smaller ventral spots at the notochord tip disappear, except for one, which persists in the finfold about halfway between the end of the ventral pigment series and the tip of the tail.

During late preflexion and flexion stages, pigment increases on the midbrain and appears on both the forebrain and hindbrain. Paired melanophores develop on the roof of the mouth below the nasal capsules and olfactory lobes, and one or more form at the tip of the lower jaw. As the pigment associated with the otic capsule increases, an embedded stripe passing through the eye region is formed (Fig. 2E). One or two surface melanophores appear posterior to the eye in the opercular region. Melanophores appear on the tip of the lower jaw, at the angle of the jaw, and later along the rami of the jaw. A large

Girella nigricans, *Medialuna californiensis*, and *Hermosille azurea*.

Species/stage	Body depth / Body length	Pectoral fin length / Body length	Pectoral fin base depth / Body length	Predorsal length / Body length	Prepelvic length / Body length
Girella nigricans					
Preflexion	17.6 ± 1.98	9.7 ± 3.00	4.3 ± 0.69		
Flexion	19.8 ± 1.58	11.3 ± 1.79	6.0 ± 0.97	54.0 ± 3.69	29.4 ± 2.83
Postflexion	23.8 ± 1.77	16.3 ± 2.42	6.3 ± 0.89	37.7 ± 4.81	33.4 ± 1.68
Juvenile	26.6 ± 1.92	21.0 ± 2.78	6.6 ± 0.34	35.3 ± 1.43	33.8 ± 1.72
Medialuna californiensis					
Preflexion	17.0 ± 2.22	10.2 ± 1.29	4.7 ± 1.44		
Flexion	22.4 ± 2.49	12.2 ± 2.05	6.8 ± 0.83	44.8 ± 6.69	34.5 ± 2.43
Postflexion	24.2 ± 2.23	16.8 ± 3.46	6.6 ± 0.72	42.4 ± 5.80	33.8 ± 2.62
Juvenile	29.3 ± 0.71	22.0 ± 1.53	6.2 ± 0.74	38.1 ± 2.12	38.1 ± 1.13
Hermosilla azurea					
Preflexion	22.5 ± 2.59	12.0 ± 0.82	7.9 ± 1.12		
Flexion	24.5 ± 2.33	12.9 ± 2.23	9.1 ± 0.83	39.4 ± 1.99	36.6 ± 0.40
Postflexion	25.8 ± 1.17	16.4 ± 4.16	7.8 ± 0.98	40.3 ± 2.42	39.3 ± 2.42
Juvenile	31.2 ± 1.50	25.0 ± 2.45	7.2 ± 0.50	40.2 ± 1.26	38.5 ± 1.91

TABLE 3.—Meristics of cleared and stained specimens of *Girella nigricans*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Length (mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Dorsal fin rays	Anal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right			Left	Right	
5.8	3	3	—	—	3	3	—	—	—	—	—	—	—
6.0	6	6	—	—	4	4	—	—	—	—	—	—	—
6.5	8	7	—	—	5	5	—	—	—	—	—	—	—
6.7	8	7	—	—	5	5	—	—	—	—	—	—	22
7.0	9	8	—	—	5	5	—	—	—	—	—	—	24
7.2	9	8	—	—	6	6	6	6	5	—	—	—	26
7.9	9	8	1	1	6	6	10	10	13	10	—	—	27
8.2	9	8	1	1	6	6	9	10	12	10	1	1	27
9.1	9	8	1	1	6	6	14	14	—	—	I,4	I,4	27
10.7	9	8	5	5	6	6	17	17	XIII,14	III,12	I,5	I,5	27
11.7	9	8	6	5	7	7	17	17	XIII,15	III,11	I,5	I,5	27
12.0	9	8	5	5	6	6	18	18	XIII,13	III,11	I,5	I,5	27
15.7	9	8	10	9	6	6	20	20	XIII,12	III,11	I,5	I,5	27
21.8	9	8	12	9	6	6	19	19	XIV,13	III,11	I,5	I,5	27
22.0	9	8	10	10	6	6	18	19	XV,13	III,11	I,5	I,5	27
37.0	9	8	11	10	6	6	19	19	XIV,13	III,10	I,5	I,5	27

melanophore appears on the isthmus just anterior to the gut, often preceded by a series of several smaller spots. The pigment on the ventral surface of the gut may also increase to form a series of pigment dashes.

At this stage a line of midlateral pigment dashes develops on the tail, posteriorly between the dorsal and ventral midline pigment. The lateral row expands anteriad, reaching the trunk by the end of flexion. Pigment becomes heaviest posteriorly, and when midlateral, midventral, and middorsal melanophores are expanded in this region, an incomplete bar is formed. Concurrent with the development of the lateral midline pigment, internal series of melanophores form above and below the vertebral column and expand anteriorly in concert with the external lateral series.

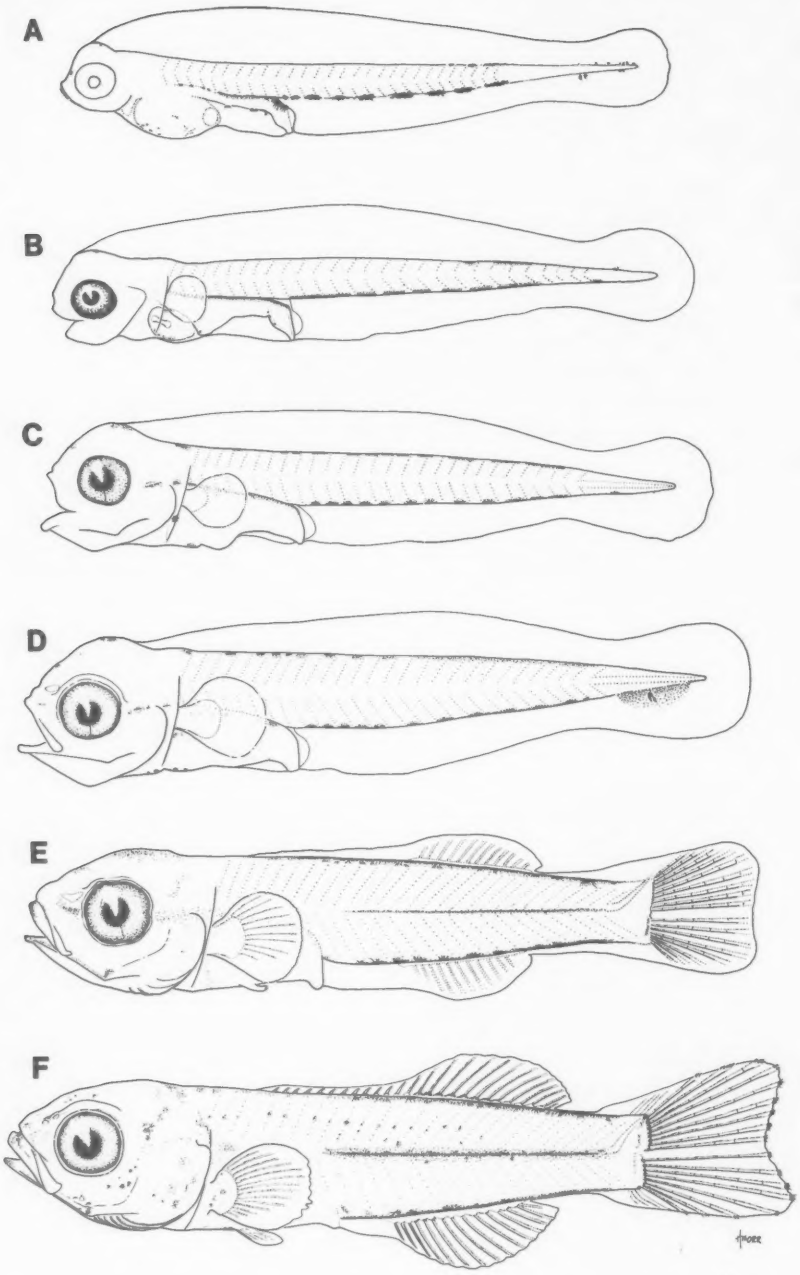

FIGURE 2.—Reared larvae of *Girella nigricans*: (A) 3.8 mm NL, day 1; (B) 3.8 mm NL, day 2; (C) 4.6 mm NL, day 8; (D) 5.3 mm NL, day 10; (E) 7.8 mm SL, day 18; (F) 10.9 mm SL, day 22.

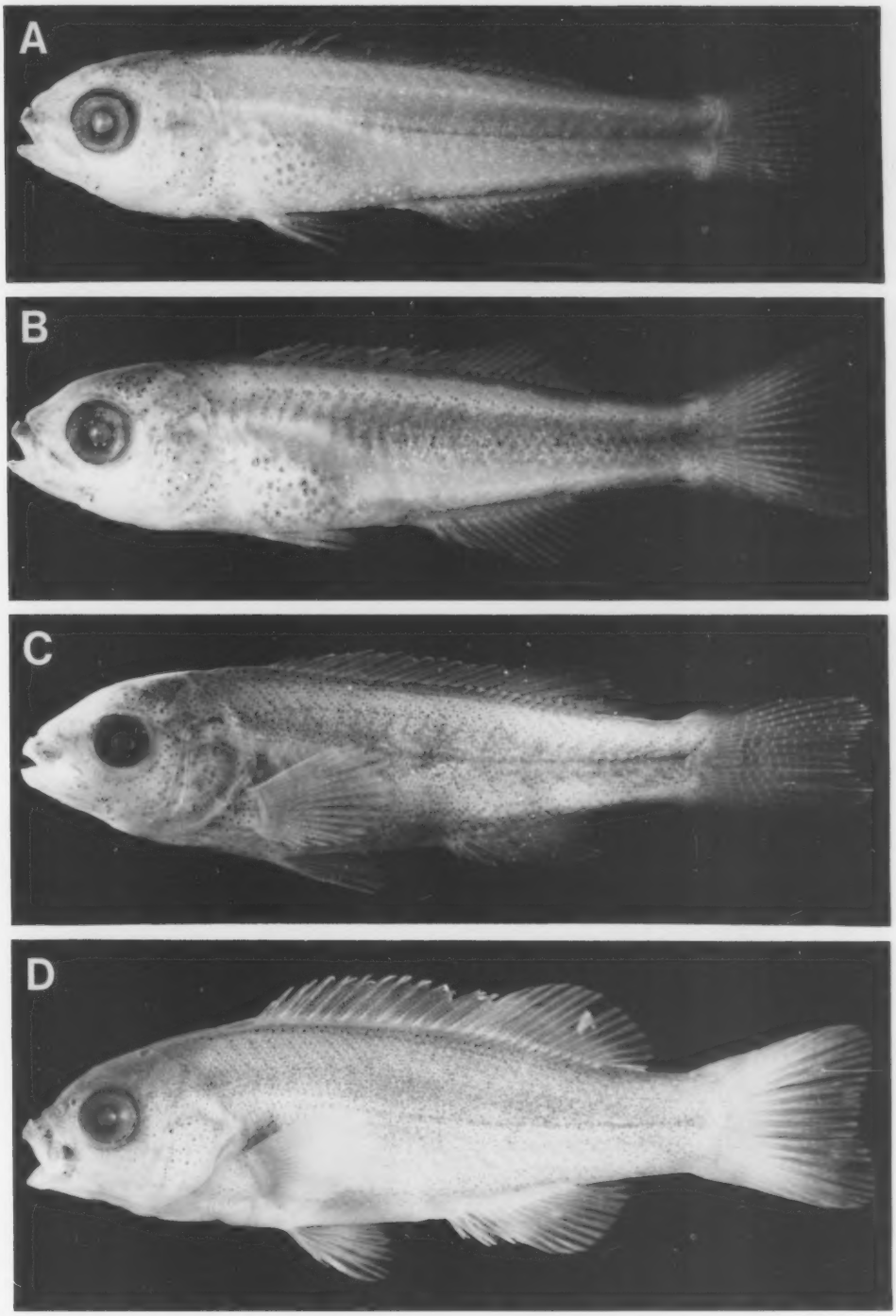

FIGURE 3.—Pelagic juveniles of *Girella nigricans*: (A) 15.8 mm SL, CalCOFI cruise 8197-JD, station 93.3.55, surface tow; (B) 17.3 mm SL, CalCOFI cruise 8107-JD, station 80.55, surface tow; (C) 22.8 mm SL, SIO Marine Vertebrate Collection, Cat. No. 76-295; (D) 29.0 mm SL, MEC SONGS cruise I-28, surface tow.

The caudal melanophore (Fig. 2D) becomes located at the posterior hypural margin between the superior and inferior elements, and remains prominent during flexion. By the end of flexion it is accompanied by 1–5 more melanophores which outline the posterior edge of the hypural plate.

By the end of flexion the sides of the gut are covered with melanophores, the dorsal midline pigment is continuous to the head, and the lateral midline series extends slightly forward of the vent. A line of pigment extends along the isthmus; pigment outlines the jaw on its ventral surface; and pigment increasingly covers the snout, dorsal surface of the head, opercles, pectoral fin bases, and the walls of the gill chambers.

During postflexion and early juvenile stages the amount of head and body pigment continues to increase. The lateral body stripe enlarges dorsad, ventrad, and anteriad. Small melanophores begin to outline the myosepta, initially in the epaxial zone and later in the hypaxial zone. Eventually the areas between the myosepta fill with melanophores and the entire body and head are covered (Fig. 3D). In addition to the development of melanistic pigment, early juveniles develop a layer of guanine which produces a silvery sheen on the lower half of the body. This silvery condition is retained throughout the pelagic phase and is lost abruptly when the pelagic young enter the tidepools at 25 mm length (Feder et al. 1974).

Fin pigment appears in early juveniles when the dorsal spines become outlined with mela-

TABLE 4.—Measurements (mm) of larvae and pelagic juveniles of *Medialuna californiensis*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Station	Body length	Snout-anus length	Head length	Head depth	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Predorsal length	Prepelvic length
5407–97.30	2.6	0.90	0.39	0.48	0.08	0.20	0.38	—	—	—	—
6607–87.55	2.8	1.2	0.60	0.58	0.08	0.22	0.44	0.30	0.14	—	—
7805–70.90	3.1	1.2	0.66	0.56	0.10	0.26	0.54	0.28	0.10	—	—
6606–90.60	3.3	1.2	0.50	0.50	0.08	0.23	0.44	0.24	0.10	—	—
6606–87.33	3.5	1.4	0.68	0.54	0.10	0.28	0.48	0.38	0.14	—	—
6907–93.30	3.8	1.6	0.84	0.74	0.22	0.32	0.68	0.44	0.18	—	—
6907–93.30	4.0	1.7	1.0	0.76	0.22	0.34	0.72	0.40	0.18	—	—
5104–107.70	4.3	1.7	0.98	0.90	0.19	0.38	0.80	0.42	0.14	—	—
6107–83.65	4.6	1.9	1.1	0.90	0.18	0.40	0.88	0.45	0.32	—	—
6207–100.45	5.0	1.9	1.2	0.96	0.24	0.44	0.84	0.60	0.20	—	—
6207–100.35	5.2	2.0	1.2	1.1	0.26	0.48	1.0	0.50	0.28	—	—
8105–100.70	5.5	2.2	1.2	1.2	0.32	0.50	1.1	0.60	0.40	—	—
5507–103.70	5.8	2.4	1.4	1.2	0.35	0.66	1.2	0.60	0.40	2.1	—
8105–100.35	6.0	2.4	1.2	1.2	0.32	0.58	1.2	0.60	0.35	—	—
6507–100.40	6.5	2.5	1.8	1.2	0.44	0.60	1.2	0.88	0.40	3.4	—
8105–100.70	6.7	2.9	1.7	1.7	0.40	0.80	1.6	0.76	0.56	3.5	—
8107–86.7.50	7.2	3.4	2.3	1.6	0.44	0.88	1.8	0.88	0.52	3.5	2.6
8108–100.40	7.9	4.0	2.4	1.8	0.64	0.88	2.0	1.3	0.48	2.9	2.8
7808–67.65	8.1	3.6	2.3	1.7	0.54	0.76	1.8	1.0	0.52	3.6	2.5
5907–103.50	8.4	4.1	2.5	2.0	0.48	0.88	2.0	1.0	0.60	3.6	3.0
7808–67.65	9.0	4.2	2.6	2.0	0.56	0.96	2.0	1.2	0.64	4.7	3.0
7808–67.65	9.2	4.1	2.4	2.0	0.42	0.96	2.0	1.3	0.64	4.1	2.9
7808–67.65	9.5	4.9	3.3	2.3	0.60	1.0	2.3	1.4	0.72	4.0	3.1
7808–93.45	9.8	5.2	3.2	2.4	0.64	1.1	2.5	1.9	0.64	4.1	3.1
5208–90.45	10.0	5.2	2.8	2.2	0.60	1.1	2.4	1.7	0.60	3.5	3.6
7808–93.45	10.8	6.0	3.5	2.7	0.72	1.2	3.0	2.4	0.62	4.2	4.1
5208–110.60	11.8	6.8	3.8	3.2	0.72	1.3	3.5	2.4	0.76	4.6	4.3
5208–110.60	12.9	7.3	4.2	3.1	0.72	1.3	3.6	2.8	0.84	5.0	5.1
7808–100.45	13.2	7.8	4.6	3.8	1.0	1.4	4.0	2.9	0.88	5.2	5.3
5208–90.45	13.5	7.8	4.7	3.8	0.96	1.5	4.0	3.3	0.96	5.3	5.2
7210–90.70	13.7	7.8	4.9	4.0	1.1	1.6	4.1	3.0	0.84	5.4	5.2
5208–90.45	17.9	9.7	5.6	4.8	1.1	1.9	5.3	4.3	0.96	6.5	6.7
7210–90.70	21.5	11.3	7.1	5.5	1.3	2.0	6.2	4.5	1.1	7.3	8.1

nophores. Gradually the fin membrane becomes covered with melanophores as does the basal half of the soft dorsal fin. Anal fin pigment is limited to a few anterior melanophores, and the caudal and the paired fins remain unpigmented.

Medialuna californiensis

Figures 1, 4, 5

General Morphology

The smallest yolk-sac larva in our collection is 2.6 mm long; it has a large oval yolk sac, a single posteriorly located oil globule (0.20 mm diameter), unpigmented eyes, and lacks a mouth (Fig. 4A). Larvae are ca. 3.0 mm long at the completion of yolk absorption; development is gradual with no abrupt changes in body form (Tables 2, 4).

The first head spines appear during flexion on the posterior preopercular margin near the angle. A 6.1 mm larva has 2 spines. The number of spines increases up to 6 in preflexion larvae and to 10–13 spines in juveniles up to 21.5 mm. In larger juveniles the spines are blunt and the posterior preopercular margin is smooth in a 33.7 mm juvenile. A single spine is present on the anterior preopercular ridge in a 6.5 mm larva. This spine is variously present or absent in flexion and postflexion larvae, and is absent in juveniles larger than 13.8 mm in our collections. A single spine is present at the edge of the subopercle in larvae as small as 7.1 mm and is found on all postflexion larvae and juveniles up to a length of 21.5 mm. An interopercular spine is present in all postflexion larvae and in juveniles up to 18.2 mm. A supracleithral spine appears late in the postflexion stage (at 10.1 mm) and a posttemporal spine appears at 12.8 mm. Both spines are present in juveniles up to 21.5 mm but are absent in larger specimens. An opercular spine is present in juveniles between 12.8 and 21.5 mm. A cleithral spine is present on a single 18.2 mm juvenile.

Notochord flexion begins at ca. 5.8 mm and is completed at ca. 8.6 mm (Table 5). Transformation into the pelagic juvenile occurs at ca. 12 mm (Fig. 5).

Fin Formation and Meristics

The first rays to form are the principal caudal rays early in flexion (Table 5). The full complement of 9+8 rays is present at midflexion, when the procurrent rays begin to develop. The full complement of 11–13 + 10–11 procurrent rays is present in early juveniles.

Dorsal, anal, and pectoral rays begin to calcify during midflexion in the manner described for *G. nigricans*. Full complements of dorsal (IX–X, 22–27) and anal (III, 17–21) rays form in early postflexion larvae (Table 5). The full complement

TABLE 5.—Meristics of cleared and stained specimens of *Medialuna californiensis*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Length (mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Dorsal fin rays	Anal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right			Left	Right	
6.1	6	5	—	—	4	4	—	—	—	—	—	—	12
6.5	9	8	—	—	6	6	—	—	—	—	—	—	21
7.1	9	8	1	1	7	7	10	10	20	II,16	—	—	24
7.4	9	8	1	1	7	6	8	8	19	14	—	—	24
8.1	9	8	—	1	6	6	6	6	9	9	—	—	24
8.6	9	8	2	2	7	7	10	10	VI,22	II,18	—	—	25
9.1	9	8	3	3	7	7	14	14	IX,22	III,18	—	—	25
9.5	9	8	4	4	7	7	14	14	VIII,22	III,17	I,2	I,2	25
10.1	9	8	5	5	7	7	14	14	X,24	III,19	I,4	I,4	25
11.0	9	8	6	6	7	7	17	17	X,23	III,18	I,5	I,5	25
12.8	9	8	9	8	7	7	18	18	X,24	III,19	I,5	I,5	25
13.8	9	8	11	10	7	7	17	17	X,25	III,19	I,5	I,5	25
18.2	9	8	13	11	7	7	18	18	X,25	III,19	I,5	I,5	25
21.5	9	8	12	11	7	7	18	18	X,25	III,19	I,5	I,5	25
27.6	9	8	12	11	7	7	18	17	X,23	III,18	I,5	I,5	25
33.7	9	8	12	11	7	7	19	20	X,23	III,18	I,5	I,5	25

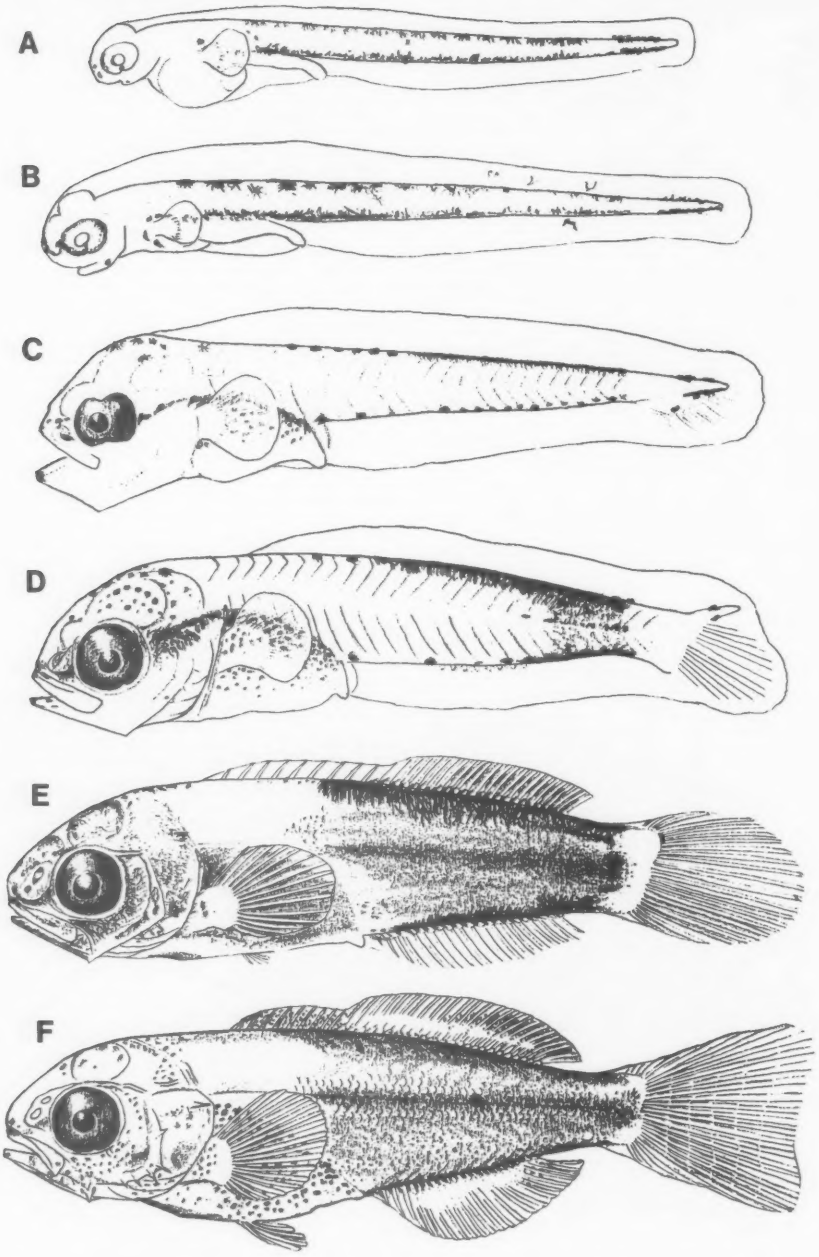

FIGURE 4.—Larvae of *Medialuna californiensis* from CalCOFI oblique plankton tows: (A) 3.0 mm NL, cruise 5004, station 120.90; (B) 3.5 mm NL, same station as above; (C) 4.7 mm NL, cruise 4906, station 102.75; (D) 6.8 mm NL, cruise 4907, station 92.68; (E) 10.1 mm SL, cruise 5007, station 100.70; (F) 11.8 mm SL, cruise 4910, station 82.77.

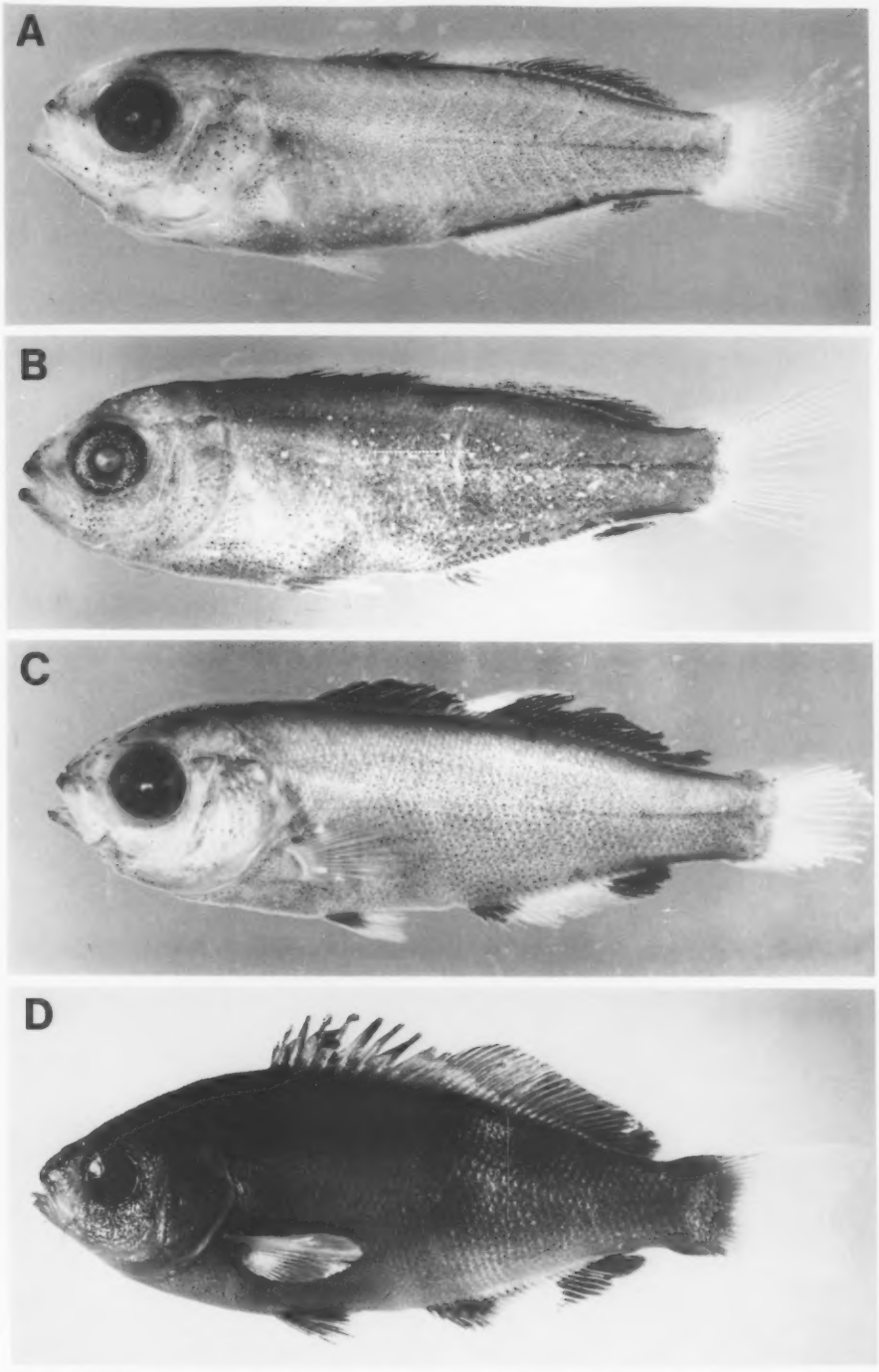

FIGURE 5.—Pelagic juveniles of *Medialuna californiensis*: (A) 13.2 mm SL, CalCOFI cruise 7808, station 100.45, surface tow; (B) 17.9 mm SL, CalCOFI cruise 5208, station 90.45, surface dipnet; (C) 20.5 mm SL, CalCOFI cruise 5407–H, station 130.60, surface dipnet; (D) 46.0 mm SL, SWFC DSJ midwater trawl, off Catalina Island, 31 October 1968.

of 17–20 pectoral rays appears at transformation. Pelvic rays begin to calcify late in postflexion and all are calcifying at transformation. Initial vertebral ossification occurs early in the flexion stage and the full complement of 25 vertebrae is present at the end of flexion. Calcification of branchiostegal rays begins late in preflexion and the full complement of 7 pairs is present in some midflexion specimens.

Pigmentation

The earliest yolk-sac larvae in our collections have extensive dorsal and ventral midline pigment. The dorsal midline has an irregular row of 30–40 melanophores between the notochord tip and the midgut region. More than 40 melanophores form an irregular series along the entire ventral margin of the tail, extending some distance forward above the gut. Melanophores in these rows coalesce to ca. 30 in each, before the eyes become pigmented. At initial eye pigmentation there are ca. 20 larger, regularly arranged melanophores in each row with a gap separating a line of 5–7 smaller melanophores that outline the dorsal and ventral margins of the notochord tip. Melanophores also appear at the dorsal surface of the gut, at the gular region, and on the snout.

At the end of the yolk-sac stage the melanophores in the dorsal and ventral rows coalesce to as few as 18 in the dorsal row and to 16 in the ventral row. A melanophore forms at the nape and, in some specimens, is continuous with the dorsal midline series. The zone of melanophores covering the dorsal surface of the gut extends forward into the head below the otic region. Embedded melanophores form in the snout region below the forebrain and some appear above the midbrain. The ventral gut melanophores move internally anterior to the gut mass. A melanophore is present at the tip of the lower jaw.

The midline melanophores coalesce further during early preflexion (15–18 dorsally and 12–15 ventrally). The short rows at the notochord tip are also reduced (2–3 dorsally and 1–3 ventrally). Melanophores are added above the brain and cover the optic lobes. Snout and otic pigment increase to give the appearance of a band through the eye, similar to that formed in *G. nigricans* and *H. azurea* (Fig. 1D, 4C). The dorsal gut melanophores increase to form a shield which extends laterally over the gut; the ventral surface of the gut remains unpigmented.

Midlateral melanophores begin to form posteriorly on the tail in preflexion larvae as small as 3.8 mm. The series consists of 1–2 (up to 4) melanophores during most of the preflexion period. During this period the dorsal midline series recedes posteriad to above the hindgut and a gap develops in the ventral series posterior to the large melanophore embedded above the anus. In late preflexion and flexion larvae the ventral series is restricted to the posterior half of the tail and contains 6–10 melanophores. Melanophores are added to the lateral series during flexion and a short bar is formed when these, together with the midline melanophores above and below, are expanded. By the end of flexion it is difficult to distinguish individual melanophores in any of the midline series. The melanistic shield on the gut covers all but the ventral midline. The dorsal surface of the head is fully pigmented and a patch of melanophores forms on the opercle. The notochord tip usually has 1–2 small melanophores dorsally and ventrally in flexion larvae, 0–2 in postflexion specimens, and 0–2 in some pelagic juveniles up to 14.5 mm in length.

The dorsal and ventral midline pigment series extend forward in postflexion larvae, the ventral series reaching the anus at ca. 9.5 mm and the dorsal series reaching the head at ca. 10.5 mm. The lateral midline series reaches the anal fin origin at ca. 9.0 mm and extends to above the midgut in transforming larvae. A covering of superficial melanophores develops on the tail and advances anteriad with the midline series. The entire body, except for the anterior trunk region, is pigmented by the end of postflexion and only a small portion of the upper trunk lacks melanophores in transforming specimens. Melanophores are added to the opercular and preopercular regions, the lower jaw, gular region, and isthmus. The entire head and gut are pigmented by the beginning of transformation.

The distinctive fin pigmentation of pelagic juveniles begins to form in late postflexion larvae when the membrane between the posterior dorsal soft rays becomes pigmented (Fig. 4E, 4F). By the end of transformation the membrane between the dorsal spines also becomes pigmented, leaving an unpigmented zone in the middle of the fin. Also, at this stage a melanistic zone develops posteriorly on the anal fin (Fig. 5A). A patch develops over the anal spines and basally on each pelvic fin in 14.0 mm pelagic juveniles; juveniles up to about 40 mm are characterized by this interrupted pattern on the median fins (Fig. 5C). In 40–50 mm juveniles the

entire dorsal fin is pigmented except for an area on the anterior half of the soft dorsal. The pelvic fins are completely pigmented at 50 mm. The pectoral and caudal fins are unpigmented in larvae and pelagic juveniles.

Hermosilla azurea

Figures 1, 6, 7

General Morphology

The size and state of development at hatching are unknown. The smallest larva examined, 2.5 mm, had pigmented eyes, a functional mouth, and no remnants of yolk or oil droplets. Preflexion larvae are moderately robust, with a coiled gut extending slightly beyond midbody (Tables 2, 6) and with a small swimbladder over the anterior gut. The head is moderately large, with a blunt snout, and with round to slightly elongate (horizontally) eyes. Development is gradual with no abrupt changes in body form or proportions. Most body parts showed small increases in size relative to the standard length (Table 2). Among the largest proportional changes are the increases in snout-anus length and in body depth (Fig. 6).

Larvae acquire only a few small head spines. The first spine may develop at the angle of the posterior preopercular margin as early as late preflexion (3.7 mm), or may be delayed until early flexion (always present by 4.7 mm); 19% of preflexion larvae had this spine. During flexion 1–3 additional small spines develop along the posterior preopercular margin and up to 3 (usually 0 or 1) small spines are acquired along the anterior preopercular ridge. Postflexion larvae may develop up to 4 very small spines along the posterior margin of the subopercular, and usually lose the anterior preopercular spines. Juveniles lack both the preopercular and the subopercular spines.

TABLE 6.—Measurements (mm) of larvae and pelagic juveniles of *Hermosilla azurea*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Station	Body length	Snout-anus length	Head length	Head depth	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Predorsal length	Prepelvic length
SONGS	2.5	1.2	0.56	0.64	0.08	0.28	0.44	0.28	0.16	—	—
	2.8	1.4	0.76	0.72	0.20	0.32	0.60	—	0.24	—	—
	3.0	1.6	0.84	0.72	0.16	0.36	0.64	0.32	0.28	—	—
	3.2	1.8	1.0	0.88	0.24	0.36	0.80	—	0.24	—	—
	3.4	1.7	0.92	0.56	0.16	0.36	0.72	0.40	0.28	—	—
	3.6	1.8	1.1	0.72	0.28	0.40	0.88	0.44	0.24	—	—
	3.8	2.1	1.2	0.96	0.32	0.44	1.0	—	0.24	—	—
	4.0	1.8	1.1	0.92	0.24	0.44	0.88	0.56	0.36	—	—
	4.4	2.1	1.1	0.92	0.28	0.44	0.92	0.52	0.36	—	—
	4.6	2.4	1.4	1.2	0.24	0.52	1.2	0.60	0.40	—	—
SONGS	4.1	2.2	1.4	1.0	0.36	0.48	1.0	0.42	0.40	—	—
	4.3	2.4	1.4	0.88	0.36	0.52	1.0	0.64	0.44	1.7	—
	4.5	2.4	1.3	1.1	0.28	0.52	1.1	0.48	0.40	1.6	—
	4.7	2.3	1.2	1.0	0.28	0.48	1.0	0.60	0.40	1.8	—
	5.0	2.6	1.6	1.2	0.40	0.60	1.3	0.48	0.48	2.0	—
	5.2	3.0	1.9	1.6	0.52	0.68	1.4	0.80	0.44	2.1	1.9
	5.4	3.2	2.0	1.4	0.48	0.68	1.5	0.80	0.48	2.3	2.0
	5.8	3.1	1.6	1.3	0.40	0.60	1.4	0.80	0.52	2.4	2.1
SONGS	6.4	3.6	1.9	1.6	0.52	0.76	1.6	1.0	0.60	2.6	2.4
SONGS	6.5	3.7	2.2	1.7	0.52	0.80	1.6	0.88	0.60	2.7	2.4
SONGS	8.6	4.9	2.5	2.2	0.68	1.0	2.2	1.7	0.68	3.3	3.4
8108–106.7.35	9.2	5.3	3.0	2.1	0.68	1.2	2.3	—	0.68	3.6	3.4
SONGS	9.6	5.5	2.9	2.6	0.68	1.1	2.5	2.0	0.64	3.7	3.9
8108–106.7.31	10.8	6.4	3.7	3.0	0.80	1.4	3.0	1.2	0.76	4.7	4.6
SONGS	14.3	8.6	4.3	3.7	1.0	1.6	4.2	4.0	0.96	5.8	5.3
SONGS	15.7	9.2	5.4	3.8	1.0	1.9	5.0	4.0	1.2	6.3	5.8
8108–120.25	17.0	9.5	5.8	4.2	1.2	2.0	5.4	4.2	1.2	7.1	6.9
SONGS	21.5	12.2	7.1	5.8	1.2	2.2	6.8	4.7	1.6	8.3	8.3

Developmental milestones occur at a relatively small size in *H. azurea*: notochord flexion begins at ca. 4.1–4.6 mm and is complete at ca. 5.9–6.3 mm; transformation to the juvenile occurs at ca. 10.8–14.3 mm (Fig. 7). Although spinous scales have been reported to occur in larvae of some Kyphosidae (Johnson 1984), juvenile *H. azurea*, as well as *G. nigricans* and *M. californiensis*, lack spines on their scales.

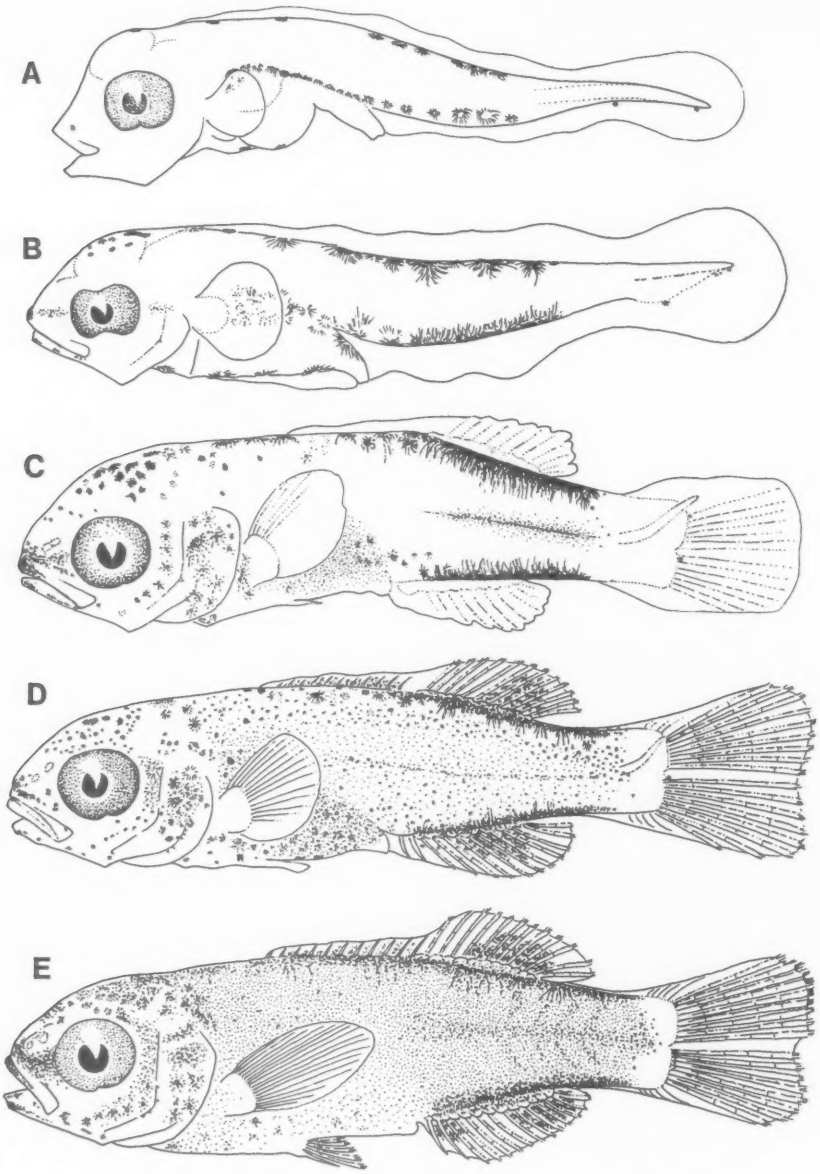

FIGURE 6.—Larvae of *Hermosilla azurea* from MEC SONGS (A–D) and CalCOFI (E) Cruises: (A) 2.6 mm NL, I–74, I-80, D–SONGS, oblique tow, 11 August 1980; (B) 4.3 mm NL, I-80, D–SONGS, surface tow, 22 September 1980; (C) 6.4 mm NL, I–53, E–LS, surface tow, 21 September 1979; (D) 8.7 mm SL, I–90, B–LS, surface tow, 27 August 1982; (E) 9.9 mm SL, 8108–NH, station 106.7.31, surface tow.

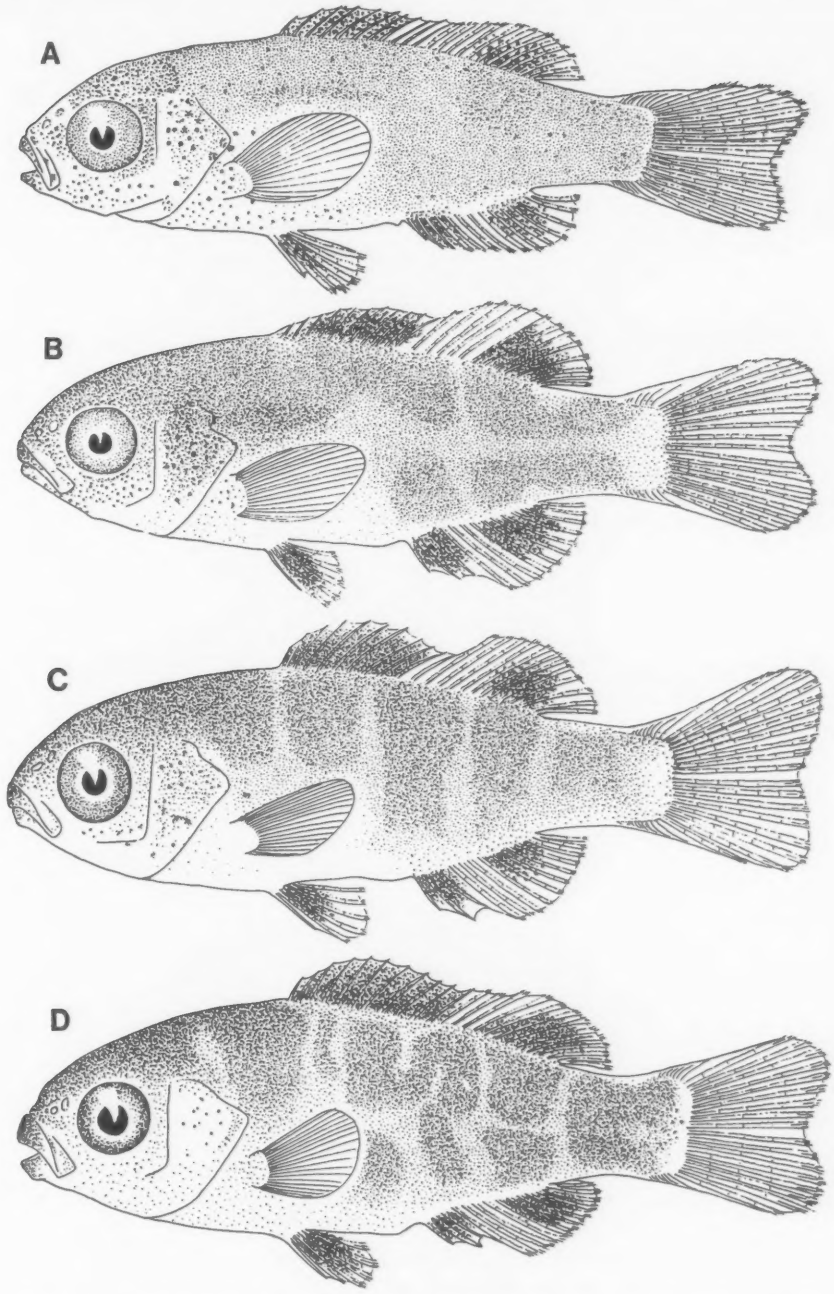

FIGURE 7.—Pelagic juveniles of *Hermosilla azurea* from MEC SONGS (A, B, D) and CalCOFI (C) surface tows: (A) 15.0 mm SL, I–35, C–1–N, 2 October 1978; (B) 16.0 mm SL, I–35, E–1–N, 2 October 1978; (C) 17.7 mm SL, 8108–NH, station 120.25; (D) 21.4 mm SL, I–35, B–1–N, 2 October 1978.

Fin Formation and Meristics

The first rays to calcify are the central principal caudal rays beginning in preflexion at about 4.1 mm (Table 7). The full complement of 9+8 principal rays is acquired during flexion at ca. 5.6 mm. Procurrent rays also may begin to calcify during flexion, as early as 5.6 mm, although more commonly they are not apparent until postflexion at ca. 6.4–6.5 mm. The full complement of 10+10 procurrent rays is completed early in the juvenile stage, by 14.3 mm.

The first dorsal and anal rays form simultaneously, early in flexion, beginning by 5.2–5.3 mm. Dorsal rays are added from anterior to posterior, with the full complement of 11 present by 5.6 mm, before the end of flexion. Dorsal spines calcify from posterior to anterior, beginning in flexion at 5.6 mm, with the full complement of 11 present in postflexion larvae by 9.4 mm. Anal rays are added from anterior to posterior, with the full complement of 10 present in flexion larvae ca. 5.3 mm long. Anal spines are added from posterior to anterior, beginning during flexion at ca. 5.6 mm; the third anal spine calcifies from the first anal ray; all three spines are present early in the juvenile stage, by 14.3 mm.

The pectoral fins initially are rounded with rounded bases, but begin to elongate during flexion when the first upper rays calcify. Addition of pectoral fin rays is from top to bottom of the fin, beginning at ca. 5.2 mm, with the full complement of 15 present by the early juvenile stage. The pelvic fins are the last to begin calcifying in the flexion stage by ca. 6.4 mm. The full complement of I, 5 rays is present by 9.4 mm.

Branchiostegal rays begin to ossify in preflexion larvae at about 4.1 mm; the full complement of 7 rays on each side is ossifying during flexion at ca. 5.2 mm. Vertebral ossification begins by 4.6 mm, just before flexion. Ossification is from anterior to posterior; all 25 centra are ossifying by the end of flexion.

Pigmentation

Preflexion larvae are relatively heavily pigmented, principally over the gut and along the dorsal and ventral midlines. In the smallest specimen examined (2.5 mm), the dorsal midline pigment consisted of a single row of 7 large stellate melanophores irregularly arranged from the midbrain to myomere 20. The number of melanophores in this dorsal row increases, so that by the beginning of flexion the dorsal and upper dorsolateral surfaces of the trunk and tail (except the last 4 or 5 myomeres) are almost completely pigmented. Dorsal and dorsolateral pigmentation on the trunk and tail becomes in-

TABLE 7.—Meristics of cleared and stained specimens of *Hermosilla azurea*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Length	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Dorsal fin	Anal fin	Pelvic fin rays		Vertebrae
(mm)	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right	rays	rays	Left	Right	
2.6	—	—	—	—	—	—	—	—	—	—	—	—	—
4.1	1	1	—	—	—	—	—	—	—	—	—	—	—
4.1	—	—	—	—	2	2	—	—	—	—	—	—	—
4.6	6	5	—	—	4	4	—	—	—	—	—	—	15
4.6	6	6	—	—	5	5	—	—	—	—	—	—	15
4.6	6	5	—	—	4	4	—	—	—	—	—	—	16
4.9	4	5	—	—	4	4	—	—	—	—	—	—	16
5.2	7	7	—	—	6	6	—	—	7	8	—	—	21
5.2	6	6	—	—	5	5	—	—	—	—	—	—	20
5.3	8	8	—	—	6	6	—	—	5	8	—	—	21
5.3	8	8	—	—	6	6	—	—	10	10	—	—	22
5.6	9	8	1	1	6	6	6	6	III,11	I,10	—	—	23
6.0	9	8	—	—	6	6	8	8	V,11	II,10	—	—	25
7.4	9	8	3	3	6	6	13	12	X,11	III,10	3	3	25
9.4	9	8	6	6	7	7	15	15	XI,11	III,10	I,5	I,5	25
22.2	9	8	10	10	7	7	15	15	XI,11	III,10	I,5	I,5	25

creasingly dense and spreads posteriorly; at the end of flexion the last three myomeres are usually unpigmented but acquire pigment by the end of the larval stage.

Midbrain pigment increases in concert with the dorsal trunk and tail pigment, covering the area over the midbrain and spreading anteriorly to the snout and posteriorly over the hindbrain. Thus, by the beginning of flexion, larvae are nearly completely pigmented along the upper surface (Fig. 1H). Snout and nape pigment are usually lighter than the remaining dorsal pigment.

Preflexion larvae have a single melanophore at the roof of the mouth; during flexion more melanophores may be added in this area. A melanophore first appears below the otic capsule in the preflexion stage (by 2.6 mm) and one develops under the anterior midbrain by 3.1 mm. Melanophores proliferate in these areas to give the appearance of a stripe through the head by, or during, flexion.

Pigment first appears on the dorsal surface of the hindbrain by 2.8 mm (one melanophore), and rapidly increases to essentially cover the dorsal surface of the hindbrain by early flexion (ca. 4.8 mm). This pigment subsequently extends posteriorly as a series of melanophores over the vertebral column.

One or two melanophores first appear at the tip(s) of the upper and/or lower jaw(s) between 2.8 and 3.1 mm. Melanophores spread along the upper jaw beginning late in preflexion or early in flexion, and along the lower jaw beginning midway or later through flexion. At ca. 2.8 mm a single melanophore appears on the gular membrane; by the beginning of flexion 3–4 additional melanophores form a longitudinal series evenly spaced along the membrane (Fig. 1G).

A single melanophore appears on the opercle late in preflexion or early in flexion (by 4.4 mm). Melanophores proliferate here to form a large pigment patch midway through flexion, and subsequently extend dorsally, ventrally, and anteriorly to cover the entire opercular area, usually by the end of flexion or early in postflexion.

The smallest specimens examined had a continuous double row of melanophores, which extended over the dorsal surface of the gut and swimbladder, and posteriorly as a single row nearly to the end of the hindgut. These specimens also had 1–6 melanophores evenly spread along the ventral midline of the gut from the anterior midgut to the anterior hindgut. The dorsal gut pigment increases, extending as far as halfway down the front and sides of the gut by the beginning of flexion, and completely covers the sides of the gut by the end of flexion. This pigment continues to spread ventrally, from anterior to posterior, meeting the midline series in postflexion larvae (between 8.6 and 9.6 mm). The series of melanophores along the ventral midline of the gut changes little during larval development. Modal numbers of melanophores in the series were 3–4 (range of 1–6) for preflexion larvae and 4 (range of 2–6) for flexion larvae.

Initially, ventral midline pigment on the tail consists of a single row of 7–10 large melanophores between the first and the 13th postanal myomeres. Usually 2 or 3 (1–4) small melanophores lie under the notochord tip; later these become located along the hypural margin (Fig. 6B, 6C). Occasionally, the first one or two postanal myomeres are unpigmented in preflexion larvae (14% of the preflexion specimens lacked pigment here), but thereafter the first postanal myomeres are always pigmented. The ventral melanophores enlarge and may increase in number during preflexion, so that by ca. 3.5 mm a melanistic band extends along the tail to ca. myomere 20 or 21.

A series of 1–3 small melanophores appears on the lateral midline of the tail at the 14th–20th myomeres late in preflexion or early in flexion (ca. 3.7–4.3 mm). Melanophores proliferate to form a band as do the ones along the dorsal and ventral midlines. Further enlargement of the ventral, lateral, and dorsal bands results in a nearly continuous tail bar during mid to late flexion. Subsequent proliferation of melanophores in this region and over the gut and trunk results in complete body pigmentation, except for the last 3–5 myomeres, by ca. midway through postflexion. Pigmentation is complete by transformation.

The dorsal and ventral midline pigment begins to spread onto the bases of the middle and posterior dorsal and anal soft rays during flexion at ca. 5.4 mm. By late flexion or early postflexion the membranes between dorsal rays 5 or 6 to 10 or 11 and between anal rays 5, 6 or 7 to 9 or 10 are pigmented. During postflexion, the base of the entire dorsal fin becomes heavily pigmented and near the end of the larval stage the membranes between the dorsal spines become pigmented (by ca. 9.6 mm). Pigmentation does not develop on the membranes between dorsal soft rays 1–5 during the larval period, and is very sparse there in juveniles. The base

of the entire anal fin is pigmented by 8.6 mm; the anal spines and membranes are heavily pigmented by 9.6 mm, as are the membranes between anal soft rays 5 to 9 or 10. The membranes between anal soft rays 1–5 are usually unpigmented in larvae, and only sparsely pigmented in juveniles.

Caudal fin pigment is usually restricted to the melanophore(s) at the distal hypural margin during the larval stage. Small melanophores may be acquired along the proximal edges of some of the principal caudal rays in small juveniles.

The first pigment on the paired fins consists of a single melanophore on the lower proximal external surface of the pectoral fin base. This melanophore may appear as early as 4.8 mm, but is not consistently present before ca. 8.6 mm. Pectoral pigment subsequently changes little, except that beginning at ca. 9.6 mm, melanophores appear at the bases of the upper pectoral rays. The pelvic fins are unpigmented in larvae but become heavily pigmented in small juveniles.

Transforming specimens are uniformly pigmented except for the residual melanistic bands at the dorsal and ventral margins and along the lateral midline of the tail. Between 11 and 14 mm, a series of faint bars begins to appear, one anterior to the dorsal fin, one below the spinous dorsal, one below the transition from spinous to soft dorsal, one below the soft dorsal, and one at the caudal peduncle (Fig. 7C). The bars are usually interrupted along the lateral midline and variously developed below the midline, giving a mottled appearance. The mottled appearance is intensified when the bars begin to subdivide and ultimately produce the 12 bars found in late juveniles and adults.

DISTRIBUTION

Girella nigricans

A total of 71 occurrences of *G. nigricans* larvae were recorded from CalCOFI oblique plankton tows during the period 1951–81 (Fig. 8). Larvae were not found on survey cruises during 1951, 1953, 1955, and 1972. Identification of some shorefish species was of variable competency during the early years of CalCOFI and this may explain the apparent absence of *G. nigricans* larvae in 1951, 1953, and 1955. Larvae ranged from San Luis Obispo, CA (cruise 6907, station 77.48) to San Cristobal Bay, Baja California (cruise 5810, station 137.23)—the former station is the only record north of Pt. Conception, CA. Thirty-eight percent of the total occurrences were between Pt. Conception and the Mexican border and 62% were off Baja California. Larvae ranged seaward to ca. 330 km (cruise 6407, station 93.70); however, 80% of the occurrences were from station 40 shoreward on the CalCOFI survey lines (typically <110 km from the coast). Numbers of larvae sorted from each sample were low, ranging from 1 to 5, with a mean of 1.35 per positive tow. The standardized mean number per positive tow was 4.0 with a range of 0.3–17.5[1]. *Girella nigricans* is a highly seasonal spawner with 80% of the larvae occurring in summer months (June, 27%; July, 45%; August, 8%). Larvae were not taken in January–March.

The importance of the surface layer as a habitat for *G. nigricans* larvae has not been assessed; however, the addition of surface (Manta net) tows on CalCOFI stations during the 1978 and 1981 surveys has provided some information. Larvae occurred in nine surface tows in 1978 and in 11 tows during 1981. These occurrences compare with those from three positive oblique tows in 1978 and one in 1981 and suggest that 1) *G. nigricans* larvae may occur frequently in the neuston and 2) they are undersampled by oblique tows. The mean size of larvae taken in surface nets is nearly twice that of larvae taken in oblique tows. The mean larval length from surface tows during 1978–81 was 7.1 mm ± 3.7 SD (range = 2.6–16.5 mm). The mean for oblique tows during 1978–81 was 3.8 mm ± 1.69 SD (range = 2.2–15.0 mm).

Medialuna californiensis

A total of 150 occurrences of *M. californiensis* larvae were recorded on CalCOFI oblique plankton tows during 1951–81 (Fig. 8). Larvae occurred on all surveys except during 1953; the apparent absence during 1953 probably was a result of identification error. Larvae ranged from off Monterey Bay, CA (cruise 5707, station 67.55) to off Pt. San Jaunico, Baja California (cruise 6507, station 133.50). There were only five occurrences north of Pt. Conception, CA, during the 30 yr period; only one of these was near the coast (Fig. 8). Except for two stations,

[1]Standardized number adjusts for percent of sample sorted and standard haul factor to give the number of larvae under 10^2 m of sea surface (see CalCOFI ichthyoplankton data reports cited in Ambrose et al. 1988).

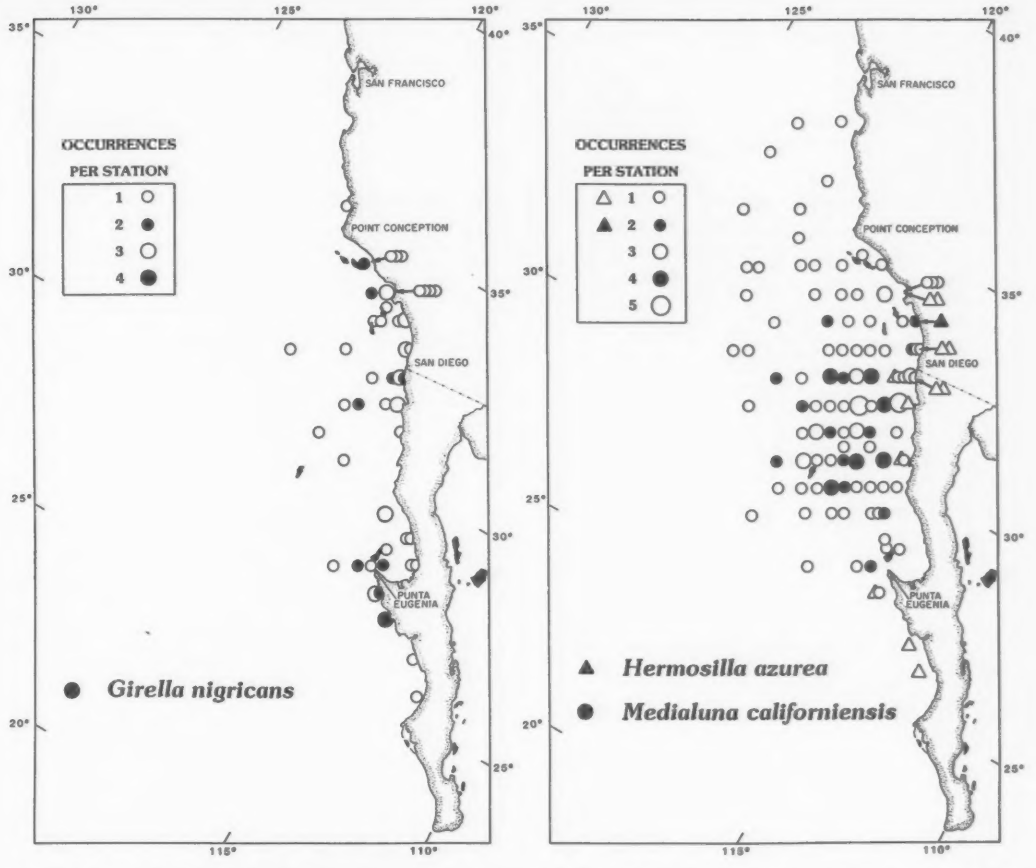

FIGURE 8.—Pooled numbers of occurrences of *Girella nigricans*, *Medialuna californiensis*, and *Hermosilla azurea* larvae taken in CalCOFI tows from 1951 to 1981. Occurrences for *G. nigricans* and *M. californiensis* represent oblique tows and those for *H. azurea* are both oblique and surface tows.

all the remaining larvae were taken between Pt. Conception, CA and Pt. Eugenia, Baja California; 28% of these occurrences were off California and the remainder were off Baja California.

In contrast to *G. nigricans* larvae, those of *M. californiensis* occur well offshore to a distance of ca. 500 km (cruise 5505, station 93.95); 71% of the occurrences were seaward of Station 40 (>110 km from the coast on most lines). Numbers of larvae ranged from 1 to 11 with a mean of 1.42 per positive tow, slightly higher than for *G. nigricans*. The standardized mean number per positive tow was 4.94 with a range of 1.0–30.7. Like *G. nigricans*, the occurrence of *M. californiensis* larvae was highly seasonal with 53% taken in July and 90% in June–August. Larvae did not occur in November–March.

Larvae of *M. californiensis*, like those of *G. nigricans*, utilize the neuston habitat and may be undersampled by oblique tows. *Medialuna californiensis* occurred only once in the oblique tows during 1978 and once in 1981, whereas there were five positive Manta tows in 1978 and three in 1981. The mean size of larvae taken in surface tows during 1978–81 was almost twice that in the oblique tows (7.0 mm ± 2.60, range = 2.6–11.0 mm versus 3.9 mm ± 1.18, range = 2.3–9.4 mm).

Hermosilla azurea

Larvae of *H. azurea* have a nearshore shallow distribution (Fig. 8). We can document only two occurrences of this species in the entire CalCOFI time series of oblique tows (cruise 6907, station 93.30, two specimens; station 97.29, four speci-

mens). Since this species was first identified during the course of the present study, it is possible that other misidentified specimens reside in the collections. They were not, however, confused with *G. nigricans* or *M. californiensis* since we have reexamined all identifications of these species. Larvae of *H. azurea* occurred in Manta net samples at three stations during the 1978 survey and at nine stations on the 1981 survey. Occurrences ranged from Santa Monica Bay, CA (cruise 8107, station 86.7.33) to Pt. San Juanico, Baja California (cruise 7807, station 133.23). Occurrences were shoreward of station 36 on each CalCOFI line (4–42 km from the coast).

Larvae of *H. azurea* were well represented in the SONGS plankton collections of MEC Analytical Systems. The shallow distribution of *H. azurea* larvae was clearly demonstrated in the SONGS collections. Surface tows accounted for 87% of the larvae and oblique tows for 14%. Larvae occurred principally in the outer section of the SONGS transect (1.9–7.2 km from the coast; ca. 18–75 m depth). Larval occurrence was highly seasonal, with 62% of the total number taken in August and >99% in July–September.

SYSTEMATICS

Johnson (1984) discussed kyphosid fishes in his review of percoid systematics and ontogeny. He considered Girellidae, Kyphosidae, and Scorpididae to be distinct families and redefined the latter to include only four genera (*Scorpis*, *Medialuna*, *Labracoglossa*, and *Bathystethus*). Evidence from adult anatomy that led to these decisions was deferred to a forthcoming review (Johnson and Fritzsche, in press). Johnson (1984) pointed out the similarity of girelline and scorpidine larvae and presented this as evidence for considering them sister groups; he now believes girellines, scorpidines, and kyphosines form a monophyletic group (G. D. Johnson[2]).

A principal problem in assessing ontogenetic characters of teleost fishes is a lack of information for all but a few taxa under consideration. This is especially true for percoids and for this group of percoids. In addition to our description of *Girella nigricans*, ontogenetic series are known for two other species of *Girella* (*G. punctata* eggs, larvae, and juveniles [Mito 1958a]; *G. melanichthys* larvae [Okiyama 1988]). Developmental stages of the other girelline genus (*Graus*) are unknown. Other than our description of *Medialuna californiensis*, the only scorpidine larval series description is that of *Labracoglossa argentiventris* (Hattori 1964). Developmental stages of two of the four kyphosine genera are known. In addition to our description of larvae and pelagic juveniles of *Hermosilla azurea* there are descriptions of developmental stages of at least three species of *Kyphosus* (*K. cinerascens* larvae and juveniles, [Mito 1958b; Okiyama 1988]); *K. sectatrix* transforming larvae and juveniles [Moore 1962]; *K. incisor* transforming larvae and juveniles [Moore 1962]; *K. vaigensis* or *bigibbus* eggs [Watson and Leis 1974]; *K. vaigensis* or *bigibbus* larvae [Miller et al. 1979; Leis and Rennis 1983]). Developmental stages of *Sectator* have not been described.

The literature on development stages of these fishes does not provide sufficient descriptive detail to adequately assess ontogenetic characters. In this paper we present detailed descriptions of representatives of the three putative families to establish a basis for character comparisons. The striking feature of the three larval series is their similarity. The fact that the three species were confused with one another during the history of CalCOFI surveys attests to this in a practical sense. Our more rigorous study of their morphologies and pigment patterns has allowed us to identify each specimen correctly, while reinforcing the similarities perceived by early CalCOFI workers. These similarities are 1) a general percoid body form with a *Girella-Medialuna-Hermosilla* grade in degree of robustness; 2) dorsal and ventral midline melanophore series, with unique variations for each species; 3) lateral midline melanophore series, with unique variation; 4) an embedded melanistic band through the eye region; 5) minute melanophores at the tip of the notochord which become associated with the hypural margin of the caudal fin; 6) an anteriad progression of general body pigmentation late in the larval period; and 7) head spination with a *Girella-Hermosilla-Medialuna* grade in degree of development. This morph is not unique among percoids (see Leis and Rennis 1983; Johnson 1984); however, the coherence of these and other more subtle characters among these three eastern Pacific species supports the argument that they represent sister groups.

The pattern of lateral pigmentation is more variable in kyphosine larvae than in girellines and scorpidines. We can recognize three pat-

[2]G. D. Johnson, Fishery Scientist, National Museum of Natural History, Washington D. C. 20560, pers. commun. April 1989.

terns of lateral body pigment in kyphosines. The pattern in *H. azurea* larvae is essentially like that in *Girella* and *Medialuna*. It begins as a midlateral series on the tail and fills in the unpigmented region above, below, and anteriad to it. In *Kyphosus sectatrix* and *K. incisor* lateral pigment extends along the entire epaxial region of the body (Moore 1962). In *K. cinerascens* and *K. vaigensis* (*bigibbus*?) larvae a broad zone of lateral body pigment expands to cover unpigmented regions above, below, anteriad, and posteriad to it (Mito 1958b; Leis and Rennis 1983).

Ontogenetic divergence among kyphosid fishes is greater during the pelagic juvenile stage than in larvae. The silvery pelagic juveniles of *Girella*, which transform abruptly to olive benthic juveniles, are well known. Apparently, *Medialuna* not only has a silvery pelagic juvenile too, but also has a strongly variegated pattern on the dorsal and anal fins. The pelagic juveniles of *H. azurea* are strongly mottled. This feature is shared with other kyphosines, some of which exhibit a striking pattern of pale spots (*K. sectatrix* and *K. incisor* [Moore 1962]; *K. cinerascens* [Mito 1958b]; *K. vaigensis* (*bigibbus*?) [W. Watson, pers. obs.]).

Ontogenetic stages of kyphosid fishes provide a promising array of systematic characters. The utility of these characters in assessing phylogenetic relationships is limited by our present inability to identify shared derived character states through outgroup comparison. The solution to this problem awaits a broader knowledge of ontogeny in kyphophids and other groups in the percoid series.

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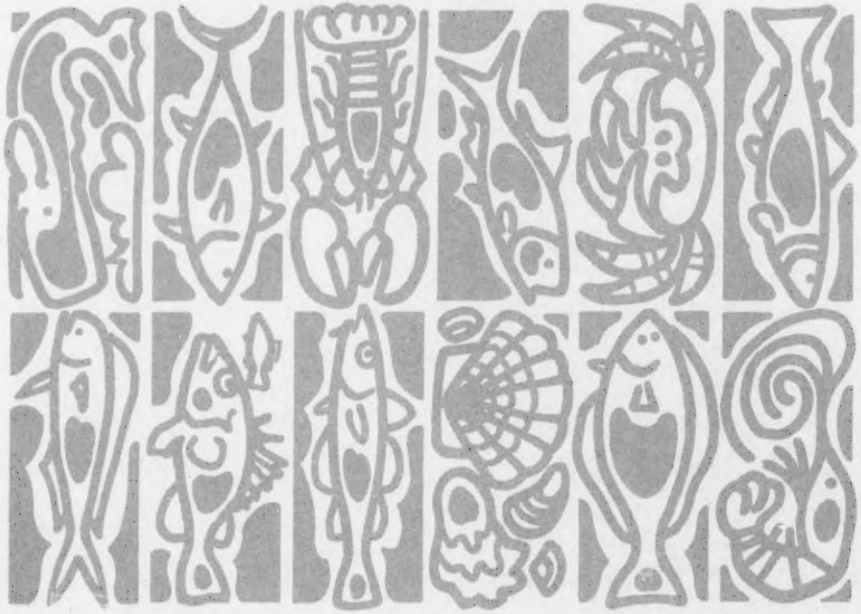
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